# THE
# JOURNAL OF
# RESEARCH ON THE
# LEPIDOPTERA

*Volume 31*          *Number 1-2*          *Spring 1992*

# The Journal of Research on the Lepidoptera

Manuscripts and Notices Material may be sent to the Editor at the above address.

The JOURNAL is sent to all members of the FOUNDATION.

---

# Biology and behavior of the neotropical butterfly *Eunica bechina* (Nymphalidae) with special reference to larval defence against ant predation.

André V. L. Freitas and Paulo S. Oliveira

Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13081-970 Campinas, São Paulo, BRAZIL

**Abstract.** This paper describes the biology and behavior of *Eunica bechina* (Nymphalidae). Eggs are laid singly on *Caryocar brasiliense* (Caryocaraceae), a plant that bears extrafloral nectaries. Most of the eggs are laid on young leaves, on which the caterpillars preferably feed. Pupation occurs off the host plant. The fifth instar larvae and pupae are like those of *Nica flavilla* and *Temenis laothoe*, suggesting that the genus is among the Callicorini. First to fourth instar larvae construct frass chains, where they rest immune from attacks by foraging ants that climb on *Caryocar* for its nectary secretions. While feeding on leaves, however, caterpillars may be killed and removed by foraging ants. When attacked by ants, *Eunica* caterpillars may repel their aggressors by regurgitating and/or bleeding. Ants receiving these fluids exhibited strong disturbance and conspicuously cleaned their mandibles and head. Dropping off the plant and hanging on the end of a drag line was also observed in *Eunica* larvae after successive bites from the ants. We suggest that frass chains are probably related to defence against "walking" predators, especially ants, who have difficulty in attacking the caterpillars at these refuges.

**KEY WORDS:** *Eunica bechina*, Eurytelinae, *Caryocar brasiliense*, cerrado vegetation, ant predation, extrafloral nectaries, herbivores, defensive behavior, frass chains

The genus *Eunica* Hübner (1819), includes 45 species and 24 additional subspecies distributed throughout the Neotropical region, the majority in the Andean Region and the Amazon Basin (Jenkins, 1990). The genus has an uncertain systematic position within the Nymphalidae (Otero, 1990) and few larvae and hostplants are known (Barcant, 1970; DeVries 1986, 1987; Ackery, 1988; Jenkins, 1990, Oliveira & Freitas, 1991). *Eunica bechina magnipunctata* Talbot 1928 occurs in the cerrados (savanna-like vegetation) of Central and Southeast Brazil (Jenkins, 1990; Oliveira & Freitas, 1991). Larvae of *E. bechina* feed on leaves of *Caryocar brasiliense* Camb. (Caryocaraceae), a plant bearing extrafloral nectaries and frequently visited by ants (Oliveira & Oliveira-Filho, 1991; Oliveira & Brandão, 1991). Early instar larvae construct frass chains (Oliveira & Freitas, 1991), a behavior also observed in other Nymphalidae, especially among the Eurytelinae and Charaxinae (Muyshondt, 1973a, b, c 1974, 1976; Muyshondt & Muyshondt, 1976; Casagrande & Mielke,

1985; DeVries, 1987; Aiello, 1991). Immature stages are still undescribed for many genera and species of Nymphalidae; studies of their morphology and behavior could help to understand the relationship among members of this family of butterflies. The present study describes the early stages of *E. bechina*. We also provide data on the natural history of immatures and adults, as well as on larval behavior and its relation to ant predation on the host plants.

## STUDY SITES AND METHODS

The study was carried out in a cerrado area in Itirapina (21°15′S, 47°49′W), São Paulo, SE Brazil during 1987, 1991 and 1992. The vegetation consists of a scrub of shrubs and trees, which is the cerrado *sensu stricto* of Goodland (1971). Average annual rainfall and temperature are ca. 1400 mm and 21°C respectively (Setzer, 1949).

A total of 27 shrubs of *Caryocar brasiliense* (35-150 cm tall) were censused to determine the preference for oviposition sites by *Eunica bechina*. The eggs were collected and the larvae were reared in plastic boxes containing leaves of *Caryocar*. Boxes were cleaned and the leaves replaced daily. Egg size is given as height and diameter; the head capsule size is the distance between the two groups of ocelli; size of cephalic horns was also measured.

The behavior of *Eunica* caterpillars and visiting ants, as well as their responses to one another, were investigated through natural and provoked encounters on *Caryocar* shrubs. Encounters were provoked by removing the caterpillars from their frass chains and placing them in the proximity of different ant species. Larvae of diferent sizes were placed on leaves or buds of ant-occupied shrubs. After the ants had encountered the caterpillar, the behavioral interactions between them were registered in observation sessions lasting 15 - 30 min. A detailed account of the ant fauna associated with *Caryocar brasiliense* is given in Oliveira & Brandão (1991).

## RESULTS

### Descriptions of early stages

Egg (Fig. 1A): yellowish, conical, and flattened at the top, with 12 to 14 longitudinal ridges and 10 to 12 transverse ridges. Average height 0.76 mm ($\sigma$=0.03 mm, n=15); average diameter 0.72 mm ($\sigma$=0.06 mm, n=15). Larvae hatch 5 days after oviposition (n=5).

First instar larva (Fig. 1B): head translucent brown, body translucent yellow changing to pale red after feeding (due to visible intestinal contents), legs and prolegs translucent yellow; maximum length 3 mm; average width of head capsule 0.42 mm ($\sigma$=0.02 mm, n=16), average duration 2.6 days ($\sigma$=0.54 days, n=47). The distribution of setae in the first instar larva is given in Fig 2A.

Second instar larva (Fig. 1C): head black with two short stubby horns; body pale brown with short conical scoli; maximum length 6 mm; average
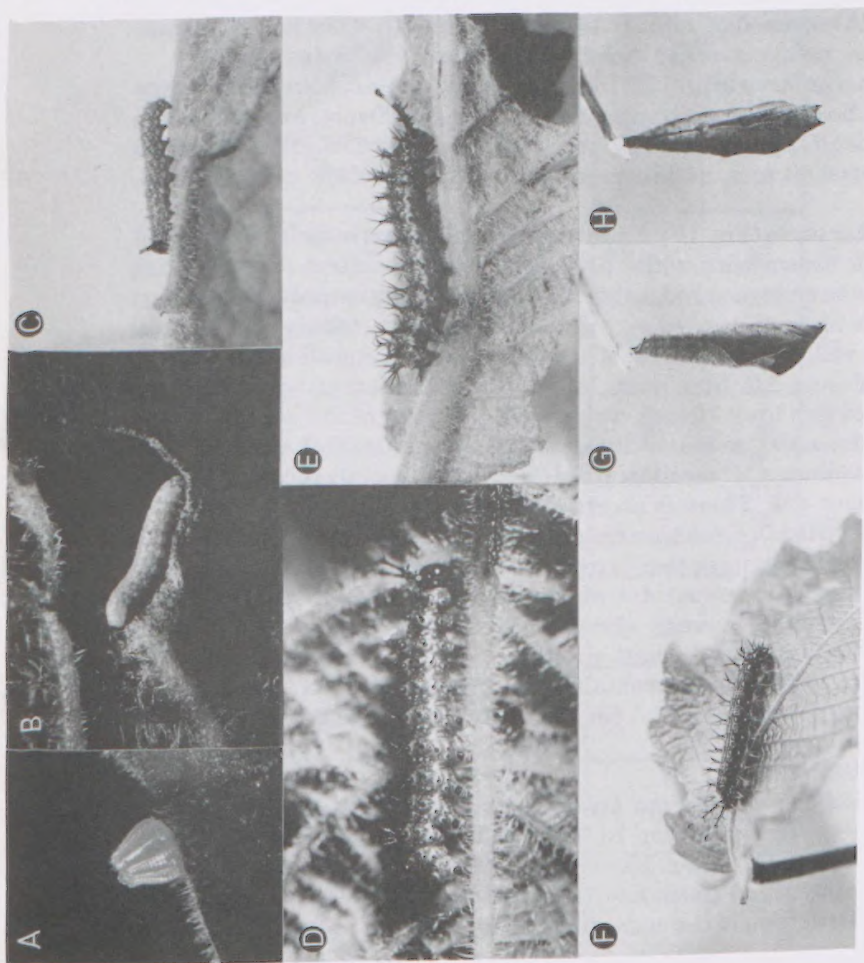
Figure 1. Immature stages of *Eunica bechina*. A, Egg. B, First instar larva. C, Second instar larva. D, Third instar larva. E, Fourth instar larva. F, Fifth instar larva. G, H, Pupa (lateral, ventral).

width of head capsule 0.67 mm (σ=0.06, n=30); average length of the horn 0.33 mm (σ=0.05 mm, n=30), average duration 1.5 days (σ=0.59 days, n=46).

Third instar larva (Fig. 1D): Head black with white warts and with two long diverging horns armed with accessory spines in the middle and ending distally in a knob crowned with short spines; body dark brown with several scoli; maximum length 12 mm; average width of head capsule 1.26 mm (σ=0.06 mm, n=43); average length of the horn 2.36 mm (σ=0.20 mm, n=43); average duration 2.4 days (σ=0.75 days, n=44).

Fourth instar larva (Fig. 1E): Head as in third instar; body dark brown with a pale brown lateral stripe; maximum length 20 mm; average width of head capsule 1.95 mm (σ=0.06 mm, n=36); average length of the horn 4.56 mm (σ=0.09 mm, n=36); average duration 3.7 days (σ=1.47 days, n=33).

Fifth instar larva (Fig. 1F): Head as in fourth instar; body brown, dorsal region dark brown with white lines and stripes, ventral region varies from yellow to orange or red, sublateral stripe orange or pale yellow, legs dark brown and prolegs red except the anal prolegs, (shiny black), scoli black with yellow and red dots. The placement of the scoli in the body is shown in Figure 2B. Maximum length 40 mm; average width of head capsule 3.28 mm (σ=0.10 mm, n=9); average length of the horn 6.62 mm (σ=0.30 mm, n=9); average duration 6.33 days (σ=1.77 days, n=12). Prepupa assumes a "J" position, fixed on the substrate by the anal prolegs and abundant silk. There is no great change in color.

Pupa (Fig. 1G,H): Green, purple or yellowish, changing to brown and gray or green after one or two days; spiracula inconspicuous light brown; a dorsal indentation separates abdomen from thorax. Abdominal segments are mobile; average size 2.2 cm (σ=0.15 cm, n=11), average duration 8.7 days (σ=1.35 days, n=18).

The sex ratio of the adults obtained in the laboratory (13 males and 9 females), can be considered 1:1 (chi square test; $\chi^2$=0.72, p>0.20; D.F.=1).

## Natural history

Females of *Eunica bechina* lay their eggs singly on small shrubs of *Caryocar brasiliense* between 10.00 and 13.00 hours. A total of 141 eggs were censused on *Caryocar*. Most eggs were found on young leaves (87%), and less frequently on shoot tips (10%), petioles (1%), and stems (1%). The vertical distribution of the eggs on the host plant varied from 3 to 150 cm above the ground ($\bar{x}$=60.5 cm, σ=44.8 cm, n=141). The caterpillars eat part of the egg shell after hatching and feed preferentially on young leaves of *C. brasiliense*. Although *E. bechina* larvae were seen on *Caryocar* from September to January (rainy season), the highest infestation level occurred between September and October when the majority of the leaves are still young, soft, and red in color.

First to fourth instar larvae of *E. bechina* construct frass chains, on the tip of which they rest (Figure 3A). When disturbed the caterpillars may
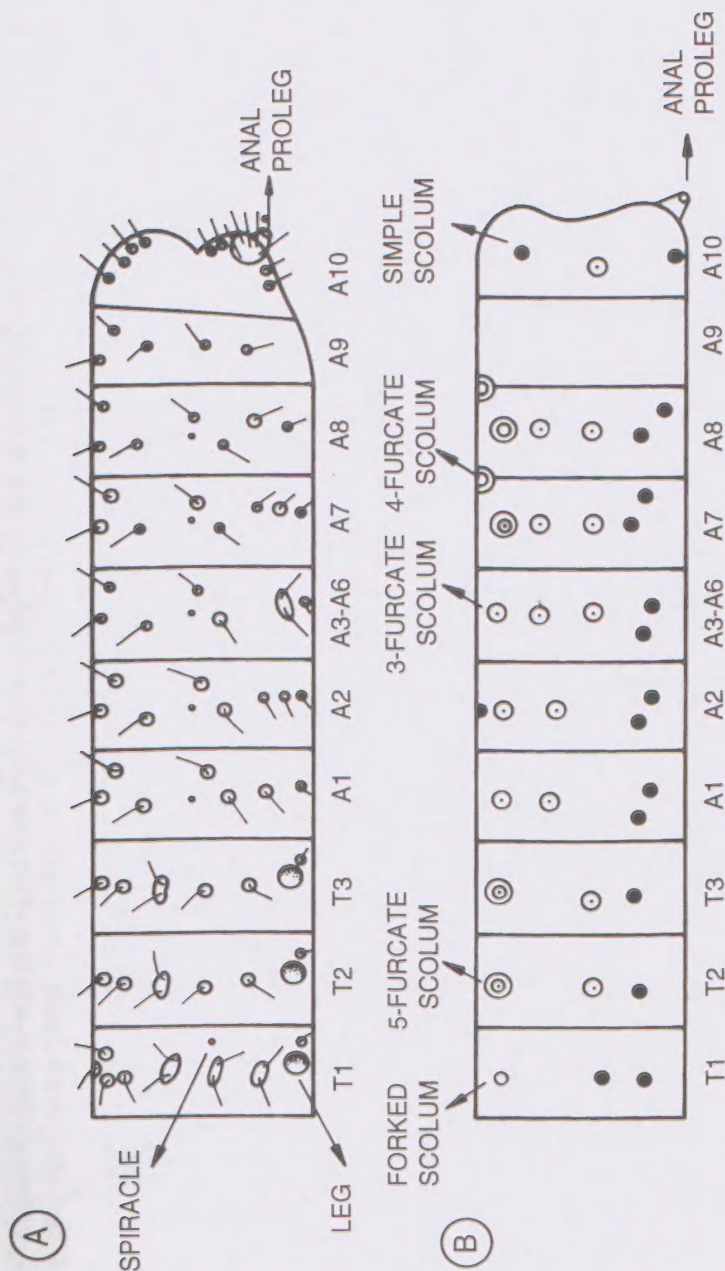
Figure 2. A, Chaetotaxy of first instar larva of *Eunica bechina*. B, Distribution of scoli in a fifth instar larva. The subdorsal 5-furcate scolum in the segment T3 is a bit larger than that of T2. The simple dorsal scolum in the segment A2 is generally absent. Many larvae may present the dorsal scoli in the segments A7 and A8 as 5-furcate.
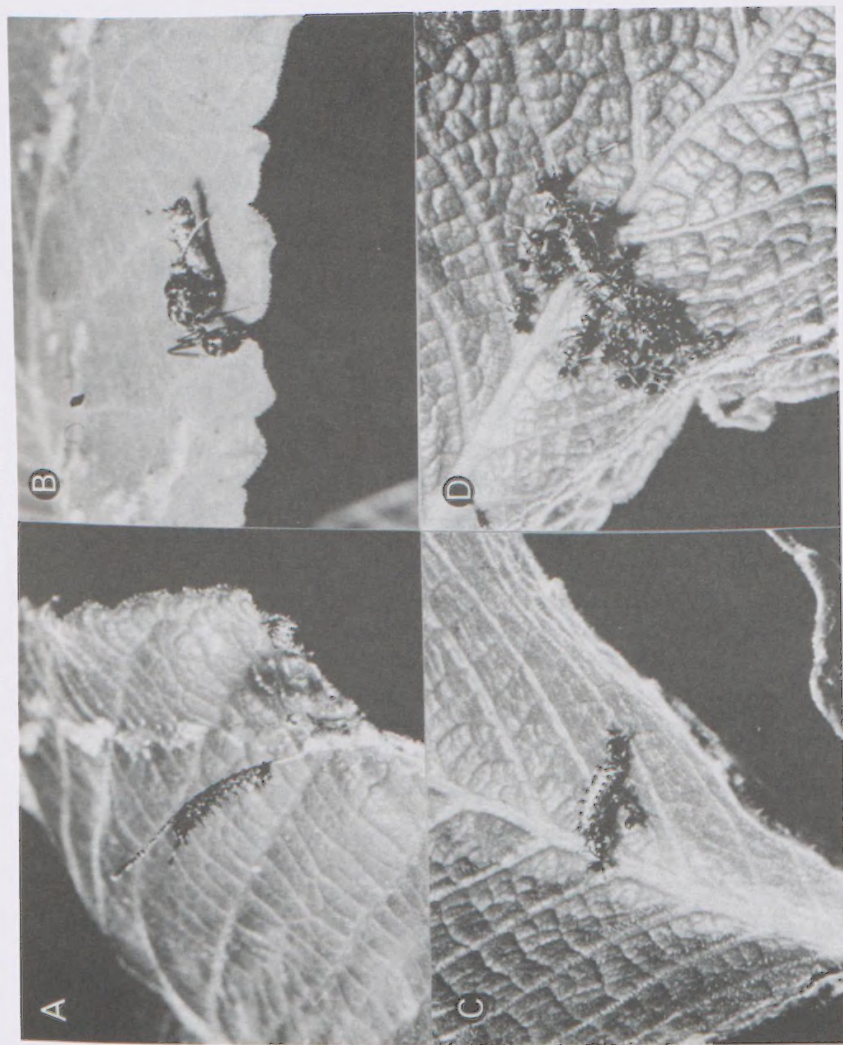
Figure 3. A, Third instar larva of *Eunica bechina* resting on a frass chain. B, Worker *Camponotus* aff. *blandus* retrieving a third instar larva. C, D, Workers of *Azteca* sp. attacking a third instar larva of *Eunica*, before and after recruitment of nestmates.

jump off the leaf suspending themselves from silk threads. Pupation usually occurs off the host plant, on neighbouring shrubs. Adults of *E. bechina* are easily seen in the field throughout the year flying about 3 m high. Agonistic behavior and chases between males of *E. bechina* are frequently observed, suggesting a kind of territoriality. The males were seen feeding on sap oozing from tree wounds, and they probably also feed on decaying fruits and mud puddles (K. S. Brown Jr., personal communication), like other "fruit feeding nymphalids" (DeVries, 1988).

### Interactions between ants and caterpillars

When not on their frass chains, *E. bechina* caterpillars may interact aggressively with the ants that climb on *Caryocar* attracted to its extrafloral nectary secretions. Behavioral interactions between *Eunica* caterpillars and ants are summarized in Table 1. In all, 47 ant × caterpillars encounters were provoked on *Caryocar* shrubs; in 36 of these the larvae were attacked by foraging ants. Such attacks resulted in the death and removal of the caterpillar from the plant in 20 instances. Two *Camponotus* species (*C. crassus* and *C.* aff. *blandus*) and one species of *Azteca* were most aggressive towards caterpillars. Unlike *Camponotus* which are large enough to subdue and carry the caterpillar alone to their nests (Fig. 3B), the small *Azteca* ants recruited tens of nestmates to help with these tasks (Fig. 3C, D).

Besides the 7 species tested against *E. bechina* larvae (Table 1), we also observed 6 other species attacking the caterpillars in the field (but without quantification), including 2 species of *Crematogaster*, 2 of *Pheidole*, one of *Pseudomyrmex* (*pallidus* group) and *Ectatomma tuberculatum* (Olivier).

Table 1. Behavioral interactions between larvae of *Eunica bechina* and ants on shrubs of *Caryocar brasiliense*. Results are based on 15-30 min of observation after provoked encounters between *Eunica* larvae and ants.

| Ant species | N° of ant × larvae encounters | N° of larvae attacked | N° of larvae removed | N° of larvae jumping of the leaf |
|---|---|---|---|---|
| *Camponotus crassus* Mayr | 15 | 10 | 6 | 3 |
| *C.* aff. *blandus* (Fr. Smith) | 10 | 10 | 7 | 1 |
| *C. rufipes* (Fabricius) | 1 | 1 | 1 | 0 |
| *C. renggeri* Emery | 2 | 2 | 0 | 1 |
| *C.* aff. *cingulatus* Mayr | 3 | 0 | 0 | 0 |
| *Azteca* sp. | 5 | 5 | 5 | 0 |
| *Zacryptocerus pusillus* (Klug) | 11 | 8 | 1 | 2 |
| Total | 47 | 36 | 20 | 7 |

When bitten by the ants, *Eunica* caterpillars frequently regurgitate and/or bleed, a behavior shown to effectively repel their aggressors who may end up abandoning the larvae. After successive bites on the larvae, attacking ants frequently exhibit strong disturbance behavior and vigorously clean their mandibles, antennae and head.

Seven larvae dropped off the plant after successive bites from the ants (Table 1). In three instances the caterpillars suspended themselves on the end of a silken line for approximately 20 min before climbing back to the leaf. Four other larvae dropped directly to the ground and hid among the leaf litter.

## DISCUSSION
### General biology

This is the first detailed description of the biology and behavior of *Eunica* immatures (see also Jenkins, 1990).

The distribution of setae in the first instar larvae is very similar to the "primitive" pattern of Nymphalidae (Nakanishi, 1988). The distribution pattern of the scoli of the fifth instar larvae and pupae is like that of *Nica flavilla* and *Temenis laothoe* (Muyshondt, 1973b, c); however, the spine distribution pattern in *N. flavilla* is quite distinctive. The pupae of *Eunica* suggest that the genus is among the Callicorini, as stated by Otero (1990), who places *Eunica* in the most advanced branch of Callicorini, paraphyletic with *Temenis* and *Nica*. However, Otero's results are based on only eight characters of adult morphology (apparently with high consistency). On the other hand, Harvey (1991) proposes that *Eunica* is related with *Myscelia, Catonephele, Nessaea, Cybdelis* and *Libythina* (this one very close to Eunica) and the paleotropical genus *Sallya* (see also Jenkins, 1990 and Otero, 1990). Further study of immatures of other Eurytelinae genera may help solve some systematic problems in this group, as has been done for the Ithomiinae (K. S. Brown & A. V. L. Freitas, in preparation).

### Defence against ants

Ants are the most frequent visitors to the extrafloral nectaries of *Caryocar brasiliense* in the cerrado (Oliveira & Oliveira-Filho, 1991; Oliveira & Brandão, 1991). Foraging ants may encounter *Eunica* caterpillars on leaves and occasionally remove them from *Caryocar*. All ant genera observed attacking *E. bechina* caterpillars are known to tend Lycaenidae and Riodinidae larvae, Homoptera, and to visit extrafloral nectaries (see DeVries, 1991; Oliveira & Brandão, 1991). *Azteca* ants, however, were also observed killing *Thisbe irenea* (Riodinidae) caterpillars (DeVries, 1991). We noted that some caterpillars can overcome predation or injury by ants through an array of behavioral mechanisms (see also Heads & Lawton, 1985; Costa et al. 1992).

The behavior of suspending themselves by silken threads is common in *E. bechina* caterpillars and appears to be widespread among the Lepi-

doptera (see also DeVries, 1987 and several citations therein). Dropping and suspending on the end of a drag line is a technique known to be employed by arthropods who live in close proximity to aggressive ants (Robinson & Valerio, 1977; Oliveira & Sazima, 1984, 1985; Heads & Lawton, 1985).

Regurgitation is also common in butterflies (see Brower, 1984). Just after attacking the caterpillars, ants receiving this fluid exhibited strong disturbance (walking erratically and shaking the body) and conspicuously cleaned their mandibles and head. Ant deterrence can also occur from bleeding by the injured caterpillars, as also noted by Heads & Lawton (1985) for some herbivores of bracken fern (*Pteridium aquilinum*). Rearing up the body, curling and wriggling vigorously (beat reflex) can intimidate or temporarily expel some predators from the plant. For some ants, however, the beat reflex may stimulate additional attacks (Malicky, 1970). These behaviors are very common among butterfly larvae, except for some Lycaenoideae (Malicky, 1970), and seem to be more effective in late instar caterpillars due to their larger size in relation to the ants (see also Heads & Lawton, 1985).

The frass chains constructed by the larvae may diminish their predation/removal by ants, since the latter were never observed climbing on this structure. The behavior of resting or taking refuge on frass chains is analogous to that exhibited by some Heliconiini larvae, which rest at the end of tendrils or on "island-like" leaf segments (Benson et al., 1976; Bentley & Benson, 1988). Frass chains are observed in several other larvae of Nymphalidae butterflies feeding on various plant families. This trait is especially common among the Charaxinae and Limenitidinae (*sensu* Harvey, 1991), a fact supporting the idea that this structure permits the utilization by *Eunica* of a plant often occupied by ants. This behavior needs to be studied in other genera of Nymphalidae such as *Hamadryas* and *Anaea*, whose larvae commonly feed on plants bearing extrafloral nectaries. Although the primary role of frass chains has not been tested so far, we suggest that it is related to defence against "walking" predators, specially ants, that would have difficulty in attacking the caterpillars on their chains.

## LITERATURE CITED

ACKERY, P. R. 1988. Hostplants and classification: a review of nymphalid butterflies. Biological Journal of the Linnean Society, 33: 95-203.

AIELLO, A. 1991. *Adelpha ixia leucas* immature stages and position within *Adelpha* (Nymphalidae). Journal of the Lepidopterists' Society, 45: 181-187.

BARCANT, M. 1970. Butterflies of Trinidad and Tobago. Collins, London.

BENSON, W. W., K. S. BROWN JR. & L. E. GILBERT. 1976. Coevolution of plants and herbivores: passion flower butterflies. Evolution, 29: 659-680.

BENTLEY, B. L. & W. W. BENSON. 1988. The influence of ant foraging patterns on the behavior of herbivores. In: Trager, J. C. (ed.): Advances in Myrmecology. E. J. Brill, New York. 297-306.

BROWER, L. P. 1984. Chemical defence in butterflies. in R. I. Vane-Wright and P. R. Ackery (eds), The Biology of Butterflies. Academic press, pp. 109-134.

CASAGRANDE, M. M. & O. H. H. MIELKE. 1985. Estágios imaturos de *Agrias claudina claudianus* Staudinger (Lepidoptera, Nymphalidae, Charaxinae). Revista brasileira de Entomologia, 29: 139-142.

COSTA, F. M. C. B., A. T. OLIVEIRA-FILHO & P. S. OLIVEIRA. 1992. The role of extrafloral nectaries in *Qualea grandiflora* (Vochysiaceae) in limiting herbivory: an experiment of ant protection in cerrado vegetation. Ecological Entomology, 17: 363-365.

DEVRIES, P. J. 1986. Hostplant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae & Nymphalidae). Journal of Research on the Lepidoptera, 24: 290-333.

—— 1987. The butterflies of Costa Rica and their natural history. Princeton University Press, Princeton, New Jersey.

—— 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. Journal of Research on the Lepidoptera, 26: 98-108.

—— 1991. Mutualism between *Thisbe irenea* butterflies and ants, and the role of ant ecology in the evolution of larval-ant associations. Biological Journal of the Linnean Society, 43: 179-195.

GOODLAND, R. 1971. A physiognomic analysis of the cerrado vegetation of central Brazil. Journal of Ecology, 59: 411-419.

HARVEY, D. J. 1991. Higher classification of the Nymphalidae (Appendix B). in H. F. Nijhout, The development and evolution of butterfly wing patterns, Smithsonian Press. pp. 255-273.

HEADS, P. A. & J. H. LAWTON. 1985. Braken, ants and extrafloral nectaries. III. How insect hebivores avoid ant predation. Ecological Entomology, 10: 29-42.

JENKINS, D. W. 1990. Neotropical Nymphalidae VIII. Revision of *Eunica*. Bulletin of the Allyn Museum, 131: 1-177.

MALICKY, H. 1970. New aspects of the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). Journal of the Lepidopterists' society, 24: 109-202.

MUYSHONDT, A. 1973a. Notes on the life cycle and natural history of butterflies of El Salvador. II A.-*Epiphile adrasta adrasta* (Nymphalidae-Catonephelinae). Journal of the New York Entomological Society, 81: 214-223.

—— 1973b. Notes on the life cycle and natural history of butterflies of El Salvador. III A.-*Temenis laothoe liberia* (Nymphalidae-Catonephelinae). Journal of the New York Entomological Society, 81: 224-233.

—— 1973c. Notes on the life cycle and natural history of butterflies of El Salvador. IV A.-*Pseudonica flavilla canthara* (Nymphalidae-Catonephelinae). Journal of the New York Entomological Society, 81: 234-242.

—— 1974. Notes on the life cycle and natural history of butterflies of El Salvador. III.- *Anaea (Consul) fabius* (Nymphalidae). Journal of the Lepidopterists' Society, 28: 81-89.

—— 1976. Notes on the life cycle and natural history of butterflies of El Salvador. VII. *Archaeoprepona demophon centralis* (Nymphalidae). Journal of the Lepidopterists' Society, 30: 23-32.

MUYSHONDT, JR. A. & A. MUYSHONDT. 1976. Notes on the life cycle and natural history of butterflies of El Salvador. I C.-*Colobura dirce* L. (Nymphalidae-Coloburinae). Journal of the New York Entomological Society 84: 23-33.

NAKANISHI, A. 1988. Study on the first instar larvae of the subfamily Nymphalinae (Lepidoptera, Nymphalidae). Special Bulletin of the Lepidopterological Society of Japan, 6: 83-99.

OLIVEIRA, P. S. & I. SAZIMA. 1984. The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Aranae: Aphantochilidae). Biological Journal of the Linnean Society 22: 145-155.

—— 1985. Ant-hunting behavior in spiders with emphasis on *Strophius nigricans* (Thomisidae). Bulletin of the British Arachnological Society, 6: 309-312.

OLIVEIRA, P. S. & A. V. L. FREITAS. 1991. Hostplant record for *Eunica bechina magnipunctata* (Nymphalidae) and observations on oviposition sites and immature biology. Journal of Research on the Lepidoptera, 30: 140-141.

OLIVEIRA, P. S. & A. T. OLIVEIRA-FILHO. 1991. Distribution of extrafloral nectaries in the woody flora of tropical communities in western Brazil. in P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (eds.), Plant-Animal Interactions: Evolutionary ecology in tropical and temperate regions. John Wiley & Sons, New York. pp. 163-175.

OLIVEIRA, P. S. & C. R. F. BRANDÃO. 1991. The ant community associated with extrafloral nectaries in the Brazilian cerrados. In: C. R. Huxley & D. F. Cutler (eds.), Ant-Plant Interactions. Oxford University Press, Oxford. pp. 198-212.

OTERO, L. D. 1990. Estudio de algunos caracteres para su uso en la clasificación de Eurytelinae (Lepidoptera: Nymphalidae). Boletin de Entomologia Venezuelano, 5: 123-138.

ROBINSON, M. H. & C. E. VALERIO. 1977. Attacks on large or heavily defended prey by tropical salticid spiders. Psyche, 84: 1-10. 10.

SETZER, J. 1949. Contribuicão para o estudo do clima do estado de São Paulo. Editora das Escolas Profissionais Salesianas. São Paulo.

# A New Method of Detection of Pebrine Disease in Tasar Silk Moth, *Antheraea mylitta* Drury (Saturniidae)

S.K. Sharan, A.K. Bansal, R.M. Shukla and K. Thangavelu

Central Tasar Research and Training Institute, Nagri 835 303, Ranchi, INDIA

In the culture of *Antheraea mylitta* Drury, a semidomesticated Tasar Silk Moth, eggs of mother moths infected with *Nosema sp.*, (microsporidian) must be discarded to avert any catastrophe on crops caused by this pathogen. The infected mother moths (pebrine diseased) are detected by a method derived from that used in sericulture (Pasteur, 1870). In this method, the abdomen of an adult is severed with scissors, placed in a small mortar, mixed with water and crushed with pestle. A drop of the smear is placed on a clean slide and examined under a microscope for *Nosema sp.*, spores. This operation is most important but also time consuming in large grainages (insectaries where pupae of *A. mylitta* in their cocoons are held and at the onset of emergence of adults, eggs produced are processed). In the present study, technique is described to shift the time of microscopic examination by examining the exuviae, which remain in cocoon shells after pupation, instead of gut examination of mother moths. The new method and its advantages are discussed.

The exuviae used in this study were from diapausing pupae of *A. mylitta* (Fig. 1) reared during August-September, 1991 on primary host plants *Terminalia tomentosa* Wright and Arnon and *Terminalia arjuna* Bedd raised at the fields of the Central Tasar Research and Training Institute, Ranchi, India. As pebrine disease can be acquired from mother moths (primary infection) or from the environment through food (secondary infection), spores of *Nosema sp.* can be detected during any stage of the life cycle. Pupae selected for this study were of three types: those raised from eggs laid by (1) pebrine infected mothers, (2) pebrine-free mothers later inoculated with *Nosema sp.* spores during mid III instar and (3) pebrine free mothers (Control). 100 males and 100 females of each type, divided into five replications, were selected. Pupae were examined side by side with their exuviae to determine presence or absence of the disease.

The specimens for microscopic examination were processed in two ways viz., a) conventional and b) centrifuge methods:

a) conventional method: pupae were first washed with distilled water for two minutes, then the lower half of the abdomen (gut) was placed in a clean mortar. The tissue was crushed and the smear examined under microscope at 675 × magnification for *Nosema* spores.

b) Centrifugal method: The respective exuviae of the pupae were crushed with 5 ml of 2 % KOH in a mortar with pestle, let stand for 3

Fig. 1    Photograph of a pupa of *Antheraea mylitta* Drury showing its cocoon shell, pupa and exuviae.

minutes, mixed and filtered. The filterate was centrifuged at 500 rpm for 30 seconds. The supernatant was decanted and made up to 5 ml. with distilled water. The same was centrifuged at 2000 rpm for 10 minutes. The sediment was then smeared on a clean slide and five fields were examined for *Nosema* spores.

Results are illustrated in Table 1. *Nosema* spores were found in the body content as well as in their exuviae of the pupae, which became infected through their mother moths. There was no difference in the percentage of infection due to conventional or centrifugal methods or between sexes. Thus, instead of gut examination of mother moths, their exuviae may be examined to eliminate those individuals which acquired pebrine disease from their mothers.

In secondary infection, *Nosema sp.* spore-bearing pupae were higher in number than in exuviae. Observations made on external symptoms of pebrinised larvae of *A. mylitta* indicate that when I or early II instar larvae are inoculated with *Nosema* spores, black spots appear on the skin of larvae of III and early IV instars, but disappears in final instar (V). This indicates a relationship with detection of *Nosema* spores in exuviae in those individuals which acquired infection during their feeding stages. The individuals which were secondarily infected by *Nosema* during different stages of their larval life require detailed and systematic study with regard to: a) time required for appearance of black spots on the skin from the time of infection, b) examination of the molted skins for infection, c) intensity of infection in various organs and their route of migration to different tissues in larvae, pupae and adults, d) difference of infection between sexes, and e) mode of entry of *Nosema* spores into eggs. Only after these studies, pupae raised from larvae infected during

Table 1. Results of Microscopic Examination of pupae and their exuviae.

| Sl. # | Type of Infection | Sex | % of pupae found Infected | | % of exuviae found Infected | | Remarks |
|---|---|---|---|---|---|---|---|
| | | | a | b | a | b | |
| 1. | Primary | ♂ | 100 | 100 | 100 | 100 | Raised from infected mother moth |
| 2. | Primary | ♀ | 100 | 100 | 100 | 100 | Raised from infected mother moth |
| 3. | Secondary | ♂ | 90 | 96 | 67 | 71 | Inoculated with *Nosema* spores in mid III instar of larval stage |
| 4. | Secondary | ♀ | 92 | 95 | 53 | 67 | Inoculated with *Nosema* spores in mid III instar of larval stage |
| 5. | Control | ♂ | 0 | 0 | 0 | 0 | Infection free |
| 6. | Control | ♀ | 0 | 0 | 0 | 0 | Infection free |

Note: (a) = Conventional and (b) = Centrifugal methods of detection of infection.

feeding in the field may be screened for *Nosema* infection in *A. mylitta* by this method.

The present accepted method of pebrine detection in grainage is solely based on adults. This includes microscopic gut examination of mother moths for microsporidia spores (Pasteur, 1870), use of India ink in the microscopic field (Geetha Bai, et al., 1985) for dry moth testing, enzyme-linked immunosorbent assay, ELISA, (Kawarabata and Hayasaka, 1987), indirect fluorescent antibody techniques, (Sato, et al., 1981, Huang et al. 1983), latex bead agglutination, (Hayasaka and Ayuzawa, 1987), fluorescent antibody technique, (Huang, 1983), slide agglutination test (Hyasaka, 1983 and Li, 1985), and monoclonal antibody detection (Zhaoxi, et al., 1990). All these methods are accurate, but are cumbersome for large commercial grainages by requiring expensive laboratory facilities and skilled personnel. Pebrine detection through microscopic examination of exuviae may help the tasar industry to produce quality breeding material.

Tropical tasar silkworm diapausing pupae are preserved from November to May in bivoltine and February to May in trivoltine races. During this preservation period, exuviae examination for *Nosema* spore bearing insects can be done in the month of May. This reduces microscopic examination activities from production time. During production time, including moth eclosion, mating, oviposition and processing of eggs, the microscopic examination of mother moths must be done during a short span of 15 to 20 days for a stock of nearly 400,000 to 500,000 cocoons. This is laborious and time consuming, therefore affecting the quality of seed

production. The new method has an advantage of distributing the grainage work evenly from May to June instead of demanding all activities during June.

## LITERATURE CITED

GEETHA BAI, M. PATIL, C.S. & KASTURI BAI, A.R. 1985. A new method for easy detection of Pebrine spores. Sericologia 25: 297-300.

HAYASAKA, S. 1983. Effect of passage in a different host insect and cell cultures on the spore surface antigens of *Nosema bombycis* (Microsporidia: Protozoa). Acta sericol. 127: 22-29.

HAYASAKA, S. & AYUZAWA, C. 1987. Diagnosis of microsporidians *Nosema bombycis* and closely related species by antibody sensitized latex. J. Seri. Sci. Japan. 56: 167-170.

HUANG, Z., ZHENG, X. & LU, Y. 1983. Detection of Pebrine Sporooan, *Nosema bombycis,* in the silkworm *Bombyx mori,* by fluorescent antibody techniques. Sci. Sericul., 9: 59-60.

KAWARABATA, T. & HAYASAKA, S. 1987. An Enzyme-Linked Immunosorbent Assay to detect Alkali-soluble spore surface antigens of *Nosema bombycis* (Microspora: Nosematidae) J. Invertebr. Pathoil. 50: 118-123.

LI, D., 1985. On the Serological diagnosis of the pebrine of silkworm, *Bombyx mori*. Sci. Sericul., 11: 99-102.

PASTEUR, L. 1870. Etudes sur la maladie des vers a soie. Gauthier-Villars, Paris. Tome I, 322 pp. Tome II, 327 pp.

SATO, R., KOBAYASHI, M., WATANABA, H. & FUJIWARA, T. 1981. Serological discremination of several kinds of microsporidians spores isolated from the silkworm *B. mori* by an indirect fluoresecent antibody technqiue. J. Sericul. Sci. Japan. 50: 180-184.

ZHAOXI KE, WEIDONG XIE, XUNZHANG WANG, QUINGXING LONG & ZHELONG PU. 1990. A monoclonal antibody of *Nosema bombycis* its use for identification of Microsprodian spores. J. Invert. Pathol. 56: 395-400.

# Direction Of Spring Migration Of *Vanessa cardui* (Nymphalidae) In Colorado

James A. Scott

60 Estes St., Lakewood, Colorado 80226

**Abstract**. Spring migration of 3016 *Vanessa cardui* (L.) migrants was studied in Colorado in 1992 and 1983, using standard vector methods. Migration was to the east-northeast/northeast (averaging 31° in 1992, 51° in 1983, east being 0° and north 90°), and this direction did not change significantly during the day, disproving a theory that migrants maintain a constant angle to the sun. The efficiency (unidirectionality) of migration is about 80% during peak migration, but drops to near zero afterward. Some spring adults in central Colo. overwintered there. Migrants mate-locate all day long, versus late in the day for non-migrants.

**KEY WORDS:** *Vanessa cardui*, migration, sun-compass mechanism.

## INTRODUCTION

The study of migration of butterflies is filled with numerous brief reports of vast swarms heading in a certain direction. There are fewer studies in which the direction of each individual was charted, and even fewer in which the time of day was recorded. The latter is of interest because of a theory that migrants fly at a constant angle to the sun Baker (1968a, b, 1969) and thus change direction from morning to afternoon. Recent migrations of *Vanessa cardui* allowed the testing of this theory.

## METHODS

Time of day and direction were recorded for each of 3016 adults: 2725 in 1992 and 291 in 1983. I walked about open areas (mostly large grassy areas) in metropolitan Denver, Colorado, during most hours on peak flight days but during only part of the day on some days, and estimated direction of each individual seen as one of 16 compass directions (N, NNE, NE, ENE, E, ESE, etc.).

Standard vector methods were used. Each observation represents an arrow of length 1, and the individual arrows can be drawn connected end-to-start (the start of the next vector connected to the pointed end of the previous vector) on graph paper. Then a line can be drawn connecting start of first vector to end of last vector, which forms the total vector whose length and angle can be measured from the graph paper (which represents the overall length and direction of migration). The following equations are a simpler way to calculate the length and direction of the total vector, where E is the number of adults flying toward the east, SSW the number flying toward the south-southwest, etc. (The derivation of the equations is this: for ENE for instance the angle is 22.5° and a vector of length 1 has a Y-component [height] of sin 22.5° or .3827 and an X-component [width] of cos 22.5° or .9239; and .70711 is the sin and cos of 45° for the NE vector, etc.)

X component of total vector= E - W + .70711(NE + SE) - .70711(SW + NW) +
    .3827(NNE + SSE) - .3827(SSW + NNW) + .9239(ENE + ESE) - .9239(WSW
    + WNW)

Y component of total vector= N - S + .70711(NE + NW) - .70711(SE + SW) +
    .9239(NNE + NNW) - .9239(SSE + SSW) + .3827(ENE + WNW) - .3827(ESE
    + WSW)

V (length of vector) = square root($X^2 + Y^2$)

By custom in mathematics, the directions and axes are arranged as in Fig. 1, and angles are counterclockwise from due east (east being 0°, north 90°, west 180°, south 270°). The overall direction of migration can be found by plotting the individual vectors, or from elementary trigonometry:
    Angle A = $\tan^{-1}(Y/X)$

The efficiency of migration is given by the length of the total vector divided by the number of adults observed (N). It represents the proportion of individuals that fly in the overall direction of migration (the directionality), and ranges from 1.0 if all individuals fly the same direction, to zero if flights are random in direction. I included in sample size only flying adults, and ignored the ones feeding on flowers or resting. Thus:
    Directionality (Efficiency) of migration E = V/N
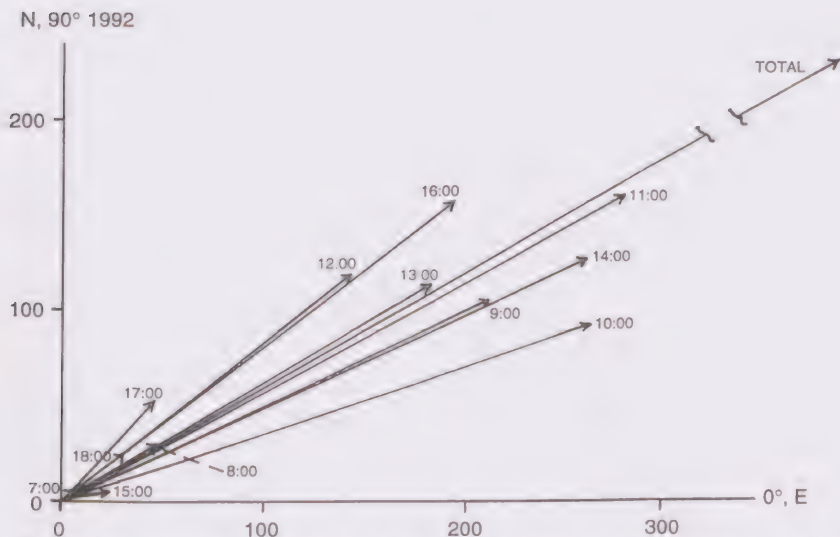    N = sample size



N, 90° 1992

Fig. 1.  Migration April 26-30 1992 during one-hour periods starting at the times indicated. A dashed line points to the 8:00 vector, and "7:00" is left of the 7:00 vector which is hidden among the bases of the other vectors. Numbers on Y and X axes represent number of migrating individuals.

## RESULTS

In 1992, very few migrants (n=13) were noted from April 10-25, which flew predominantly eastward. A vast migration occurred April 26-30, few were seen May 1-2, a small migration occurred May 3, few May 4-5, few (N=18) flew northeastward May 6, and very few (N=8) flew predominantly northeastward May 8-18. Table 1 details migration from April 26-May 5. The April 26-30 peak was massive (especially April 28-30), the overall direction for the five days was a little north of ENE (31°, V=1945., N=2395), and efficiency was great (81%). May 1 the migration was ceasing (flying to NNE with only 50% efficiency), and May 2 the few adults seen were essentially nonmigratory with a very small vector and almost zero efficiency. May 3 a small migration (N=167) again occurred, but oddly its direction was southeastward at high efficiency (79%). May 4-5 few adults were seen and most were nonmigratory judging by the low efficiency (36% and 24%); they flew predominantly eastward May 4 indicating perhaps a mixture of southeastern migrants like the day before and northeastward migrants like the next day May 5 when they flew northeastward as before.

Table 1. Daily migration 1992, N=2725.

| Day | N | Direction | Vector | Unidirectionality |
|---|---|---|---|---|
| April 26 | 57 | 25.02° | 40.27 | .71 |
| April 27 | 124 | 16.52° | 104.66 | .84 |
| April 28 | 1065 | 29.25° | 882.09 | .83 |
| April 29 | 474 | 39.51° | 382.63 | .81 |
| April 30 | 677 | 30.26° | 543.17 | .80 |
| May 1 | 53 | 63.89° | 26.65 | .50 |
| May 2 | 20 | 19.75° | 1.06 | .05 |
| May 3 | 167 | 320.34° | 132.08 | .79 |
| May 4 | 23 | 357.87° | 8.24 | .36 |
| May 5 | 26 | 41.81° | 6.28 | .24 |

Table 2. Migration each hour April 26-May 5, 1992, N=2683. Times are military standard time of start of one hour periods (7:00 means 7:00-7:59).

| Hour | N | Direction | Vector | Unidirectionality |
|---|---|---|---|---|
| 7:00+ | 20 | 45.84° | 5.18 | .26 |
| 8:00+ | 75 | 33.94° | 53.73 | .72 |
| 9:00+ | 286 | 28.28° | 241.11 | .84 |
| 10:00+ | 361 | 22.35° | 295.22 | .82 |
| 11:00+ | 373 | 30.10° | 321.60 | .86 |
| 12:00+ | 223 | 40.40° | 185.51 | .83 |
| 13:00+ | 282 | 31.38° | 218.47 | .77 |
| 14:00+ | 422 | 23.12° | 307.54 | .73 |
| 15:00+ | 157 | 328.94° | 113.10 | .72 |
| 16:00+ | 335 | 35.29° | 250.15 | .75 |
| 17:00+ | 109 | 49.12° | 68.19 | .63 |
| 18:00+ | 40 | 39.54° | 38.98 | .97 |

| Table 3. Migration each hour April 26-30, 1992, N=2395. | | | | |
|---|---|---|---|---|
| Hour | N | Direction | Vector | Unidirectionality |
| 7:00+ | 19 | 45.71° | 6.18 | .33 |
| 8:00+ | 75 | 33.94° | 53.73 | .72 |
| 9:00+ | 274 | 26.71° | 238.13 | .87 |
| 10:00+ | 317 | 19.42° | 277.88 | .88 |
| 11:00+ | 373 | 30.10° | 321.60 | .86 |
| 12:00+ | 223 | 40.40° | 185.51 | .83 |
| 13:00+ | 268 | 31.52° | 214.07 | .80 |
| 14:00+ | 361 | 26.27° | 289.26 | .80 |
| 15:00+ | 27 | 10.24° | 20.24 | .75 |
| 16:00+ | 309 | 39.85° | 249.05 | .81 |
| 17:00+ | 109 | 49.12° | 68.19 | .63 |
| 18:00+ | 40 | 39.54° | 38.98 | .97 |
| Total | 2395 | 30.77° | 1944.63 | .81 |

| Table 4. Migration 1983, in two-hour periods. | | | | |
|---|---|---|---|---|
| Hour | N | Direction | Vector | Unidirectionality |
| 8:00+ | 45 | 51° | 11 | .25 |
| 10:00+ | 61 | 45° | 25 | .41 |
| 12:00+ | 55 | 59° | 34 | .61 |
| 14:00+ | 73 | 54° | 49 | .67 |
| 16:00+ | 57 | 42° | 42 | .74 |
| Total | 291 | 51° | 161 | .55 |

In 1983, a few adults were seen April 22-24, with a moderate migration April 25-27, few migrants April 28-30, and a small migration May 4. The overall direction of migration was to the northeast (51°, Table 4, Fig. 2).

Evidently the southwestern deserts such as the Mojave and Sonoran Deserts are the major source for spring *V. cardui* in central Colorado, if the butterflies maintained the same ENE-NE flight in Arizona-Utah-California that they flew in Colorado.

Migration in insects is generally considered to be "post-teneral, pre-reproductive" (Johnson, 1969), although there are a few observations of oviposition then continuing migration, and oviposition during north-ward migration is typical of *Danaus plexippus* (L.)(Cockrell et al. 1993); thus migration obviously starts after the cuticle is hardened for flight, and stops as the eggs become ready to be laid. This generalization seems true for *V. cardui* also, because the relative lack of migration on some days in 1992 (May 1-2, 4-5) suggests that adults had stopped migrating then, presumably to reproduce (several ovipositions were observed April 28 by a nonmigrating female).

In 1983 the efficiency of migration gradually increased during the day (Table 4), evidently because mornings were cool and adults often fed on flowers in the morning. But in 1992 efficiency was about the same all day (Tables 2-3) except very early in the morning, probably because mornings were warmer in 1992.
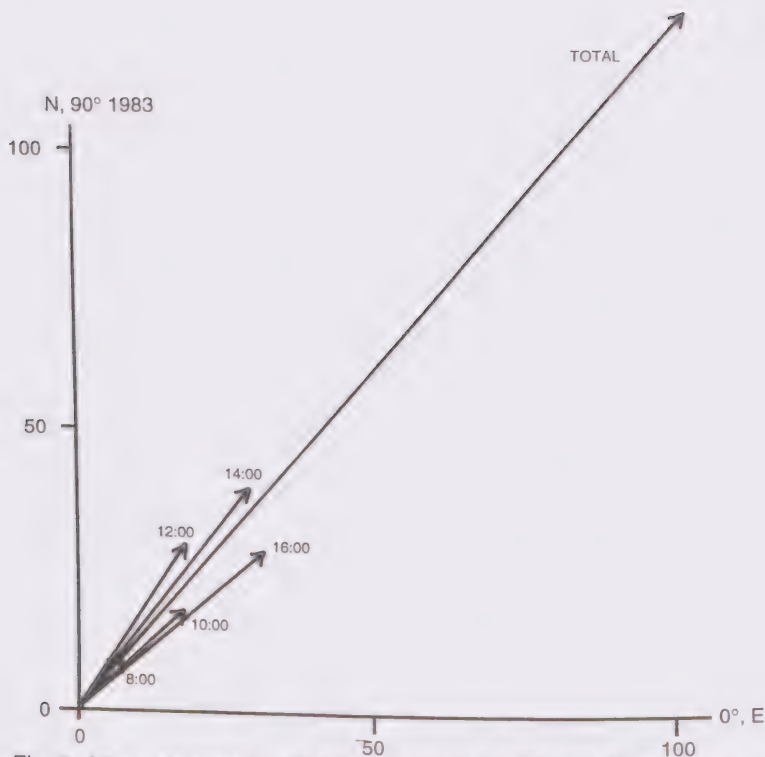
Fig. 2. Migration 1983 during two-hour periods starting at the times indicated.

## The butterfly sun-compass mechanism

Baker (1968a, b, 1969) claimed that butterflies migrate by maintaining a constant angle to the sun, so that their direction changes clockwise during the day in northern latitudes where the sun's position moves east to south to west during the day. *Vanessa cardui*, however, does not change its direction of migration during the day (Tables 2-4, Figs. 1-2). Adults flew a little north of ENE in 1992, NE in 1983, with no significant change of direction during the day. Obviously *V. cardui* has some neurological mechanism that produces a constant direction of flight during the day despite the change of direction of the sun as it moves across the sky. Probably this mechanism is the same sun-compass clock that has been demonstrated in honeybees.

The main difference between the observations of Baker and my own is that Baker recorded flight directions in ordinary populations that were not in migratory flight, and then assumed (wrongly) that their behavior was like that of migratory butterflies, whereas my observations are of obvious, definite migrations. My opinion is that Baker's observations of nonmigratory butterflies showed a change in direction during the day because glare from looking toward the sun affected the ability to notice

butterflies flying in certain directions, causing a systematic bias that followed the change of direction of the sun during the day. Possibly some non-migratory butterflies do change direction somewhat during the day, but this seems doubtful. Since no other authors have proved any significant change of direction of migration during the day, and other studies proved that direction does *not* change during the day (Arbogast 1966 on *Agraulis vanillae*, Balciunas & Knopf 1977 on *Urbanus proteus*, Walker 1978 on *Precis coenia*, *Phoebis sennae*, K. Adams in Baker 1978 on *Belenois aurota*, D. Lawrie 1984 Lepid. News #1 p. 7 and M. Myres Can. Field Nat. 99:147-155 on *Vanessa cardui*), clearly Baker's theory must be discarded.

To more-objectively determine the sun's influence on observer bias, and to obtain more accurate data, more sophisticated apparatus will be necessary: the observer would sit on a platform that rotated frequently, and would note for each migrant the compass angle printed on a surrounding deck and enter it into a computer, while the computer recorded the angle of the observer's seat to the sun; the computer would use the time of day to calculate the angles of butterfly and observer to due north, and the number of adults seen at each direction could be compared to the angle of observer to the sun to determine any observer bias.

## Adult overwintering in Colorado

Most authors have perhaps wrongly assumed that *V. cardui* overwinters only in southern areas like SW Arizona and Mexico (Williams 1970). But in central Colorado, my 30 years' observations suggest that adults almost *never* migrate southward; the very few southward migrations that have been observed were high in the mountains in midsummer (Emmel & Wobus 1966 in Colo., and I saw a southward migration in the alpine zone of Wind River Mts. Wyo. early Aug. 1983 and another in alpine central Colo.). Southward migration has never been seen on the Colorado plains/foothills, where every year during September large numbers nectar on *Chrysothamnus nauseosus* and other flowers until frost, *without* migrating. When wild-caught Sept. adults are placed in a home freezer, they die no earlier than the other *Vanessa*, *Polygonia*, and *Nymphalis* which are known to overwinter as adults (all die within 30 minutes in the freezer, suggesting that adults in nature must require many hours days or weeks of gradually colder temperatures to increase their internal concentration of glycerol to survive freezing). In addition, adults are generally present in spring even in years without noticeable in-migration, and Cockerell (1934) once found an adult in January in nature in Boulder Co. Colo. Evidence that *V. cardui* overwinters in Britain, where it was once thought to be just a temporary migrant, has been found (Baker 1978).

But analysis of wing length proves that many spring adults must be migrants from southward. In Europe, spring adults average smaller than summer adults (Baker 1978), because smaller adults bred in the

south migrate north in spring. This is also true in central Colo., where forewing length in the months from April-Oct. averages 28.9, 28.0, 29.6, 32.6, 31.2, 32.1, 31.4 mm. The main change in size is about mid June, thus April-June 10 adults average 28.1 mm (S.D. 2.9, range 21-33, N=59), whereas June 17-Oct. adults average 31.8 mm (S.D. 2.0, range 25-37, N=182). This highly significant difference (P<.01) proves that spring Colo. adults must be supplemented by migration from the south, because if spring adults were solely overwinterers they would have the same forewing length as the adults the previous fall. But some adults are large in spring (32-33 mm in both April and May) and variation in size is greater in spring (larger S.D.), and these large adults still could be overwinterers.

Probably adults hibernate in central Colorado every year, as in Europe where Baker (1978) concluded that "each autumn some individuals enter hibernation throughout the breeding range." The strength of spring versus fall migrations is reversed between *V. cardui* and *D. plexippus*: *V. cardui* migrates strongly in spring and weakly or not at all in fall, while *D. plexippus* migrates slowly northward in spring over a period of several generations, strongly southward during one generation in fall (Cockrell et al. 1993). Thus migration in *V. cardui* should not be viewed as a strictly seasonal movement like that of *Danaus plexippus*; it must be viewed also as a population outbreak in which during a few outbreak years adults fly to regions (mostly northward in spring) where prospects of rearing offspring are presumed to be better.

## Mate-locating behavior

When not migrating, *V. cardui* males mate-locate (chase others and court) only late in the day, preferably late afternoon-early evening. But during migrations they mate-locate all day: the number of chases seen each hour of migration in 1983 & 1992 was 8:00 (8:00-8:59)-4, 9:00-16, 10:00-18, 11:00-15, 12:00-12, 13:00-9, 14:00-18, 15:00-12, 16:00-25, 17:00-14, 18:00-14. No courtships were seen. Many migrations would be toward regions with a low population of adults, so mating en route seems preferable to waiting until arrival and gambling on the presence of a suitable mate there.

## Flower-feeding behavior

Adults—presumably both migratory and nonmigratory—often fed during the migrations. Yellow and white flowers may be preferred (although this may be an artifact since cultivated purple *Buddleja davidii* is enormously popular). Number of visits and flower color were: *Taraxacum officinale* (yellow) 190 visits, *Syringa vulgaris* (blue) 45 (white) 1, *Prunus cerasus* (white) 24, *Prunus virginiana melanocarpa* (white) 14, *Penstemon secundiflorus* (blue) 6, *Malus* sp. crabapple (pink) 7, *Astragalus drummondii* (white) 4, "pot of gold" mustard (yellow) 4, *Erigeron compositus* (white) 3, *Thlaspi arvense* (yellow) 3, *Prunus pissardi*

*rosea* (white) 2, *Cryptantha minima* (white) 2, *Malus sylvestris* 2 (white), *Erysimum* (yellow) 2, *Oxytropis lamberti* (purple) 1.

## LITERATURE CITED

ARBOGAST, R., 1966. Migration of *Agraulis vanillae* in Florida. Fla. Ent. 49:141-145.

BAKER, R. R., 1968a. A possible method of evolution of the migratory habit in butterflies. Phil. Trans. Roy. Ent. Soc. London (B) 253:309-341.

———, 1968b. Sun orientation during migration in some British butterflies. Proc. Royal Ent. Soc. London (A), 43:89-95.

———, 1969. The evolution of the migratory habit in butterflies. J. Anim. Ecol. 38:703-746.

———, 1978. The evolutionary ecology of animal migration. Holmes & Meier Publ. Inc., N. Y., 1012 p.

BALCIUNAS, J. & K. KNOPF, 1977. Orientation, flight speeds, and tracks of three species of migrating butterflies. Fla. Ent. 60:37-39.

COCKERELL, T. D., 1934. Pyrameis cardui on New Year's Day. Ent. News 45:174.

COCKRELL, B., S. MALCOLM, & L. BROWER, 1993. Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. Pp. 233-251 In: Biology and conservation of the monarch butterfly, S. Malcolm and M. Zalucki eds., No. 38 Science Series, Nat. Hist. Mus. Los Angeles County.

EMMEL, T. C. & R. A. WOBUS, 1966. A *southward* migration of *Vanessa cardui* in late summer and fall, 1965. J. Lepid. Soc. 20:123-124.

JOHNSON, C. G., 1969. Migration & dispersal of insects by flight. Methuen & Co. Ltd., London, 763 p.

WALKER, T., 1978. Migration and re-migration of butterflies through north peninsular Florida: quantification with malaise traps. J. Lepid. Soc. 32:178-190.

WILLIAMS, C. B., 1970. The migrations of the painted lady butterfly, *Vanessa cardui* (Nymphalidae), with special reference to North America. J. Lepid. Soc. 24: 157-175.

# Spread of the Southern African Lycaenid butterfly, *Cacyreus marshalli* Butler, 1898, (LEP: Lycaenidae) in the Balearic Archipelago (Spain) and considerations on its likely introduction to continental Europe

Victor Sarto i Monteys

Servei de Protecció dels Vegetals. DARP. Generalitat de Catalunya. Bruc, 90. 08009 Barcelona, Spain.

**Abstract.** The establishment of the lycaenid butterfly *Cacyreus marshalli* on the island of Majorca (Spain), originating from southern Africa, has already been reported (Eitschberger & Stamer, 1990; Sarto i Monteys & Masó, 1991). The latter warned of the likelihood of this species being introduced to neighbouring areas, particularly the north-eastern coast of Spain (the Communities of Valencia and Catalonia) and the other islands of the balearic archipelago.

The present work reports the finding of this species on the islands of Menorca and Ibiza and its apparent absence, for now, from the island of Formentera. Its present status in the archipelago is discussed with the likelihood of invading the Iberian Peninsula and the european continent.

**Resumen.** El establecimiento del licénido *Cacyreus marshalli* en la isla de Mallorca, procedente de Africa meridional, ya había sido constatado en trabajos anteriores (Eitschberger & Stamer, 1990; Sarto i Monteys & Masó, 1991). En éstos se advertía de la posibilidad de que esta especie fuera también introducida en áreas cercanas principalmente en las zonas costeras valencianas y catalanas, y por supuesto, en las restantes islas que conforman el archipiélago balear.

En el presente trabajo se da cuenta del reciente hallazgo de esta especie en las islas de Menorca e Ibiza así como, por el momento, de su ausencia en la de Formentera. Asimismo se hacen algunas consideraciones sobre el estado actual de la especie en el archipiélago balear y se comenta la posibilidad de que invada la Península ibérica y el continente europeo.

## INTRODUCTION

The establishment of a breeding population of the african lycaenid, *Cacyreus marshalli* Butler, 1898, on the island of Majorca (Spain) was first confirmed by Sarto i Monteys & Masó (1991), though it had been previously suspected by Raynor (1990) and Eitschberger & Stamer (1990). The latter also made the first correct identification of this introduced species. Data on its biology on Majorca were first reported by Sarto i Monteys & Masó (1991), Masó & Sarto i Monteys (1991) and more recently by Sarto i Monteys (1992). This species may become a serious

pest of cultivated geraniums (*Pelargonium*), should proper control measures not be taken as has already happened in Majorca.

As a result of its recent discovery on the islands of Menorca and Ibiza, comments will be made on its present status in the archipelago as well as on the likelihood of it invading the Iberian Peninsula and the European mainland.

## NEW DATA ON DISTRIBUTION

During Easter 1992, two very worn males were caught within a residential area known as 'La Dehesa', north of Castellón de la Plana, in the Autonomous Community of Valencia. This region is by the sea and has abundant ornamental geraniums. The specimens were sent to Dr. Fidel Fernández Rubio, who identified them as *C. marshalli* (Fernández Rubio, pers.comm.). These represent the first record in the wild of this species in the Iberian Peninsula and the second in the European mainland. A male specimen had been found in Brussels (Belgium) on August 3, 1991 (Troukens, 1991).

However, the history of the introduction of this species into Europe goes back to November 1978, when two caterpillars were found in Cheshunt, Hertfordshire (United Kingdom). Those had been accidentally imported on *Pelargonium* plants var. 'Fever Cascade', which had originated from the Republic of South Africa. The larvae were impounded and eventually completed their larval development at the laboratories of the British Ministry of Agriculture, Fisheries and Food (MAFF) in Harpenden, Hertfordshire. Figure 1 shows a map of Western Europe indicating where the species has been found. Figure 2 shows the islands of the Balearic archipelago and the surrounding coasts of the Valenciana and Catalonian communities.

In October 1990 Ulf Eitschberger and Paul Stamer correctly identified the species for the first time from specimens collected by the latter in Paguera (Majorca) in November 1989. They suggested the butterfly or its first instars had been introduced with the foodplants and became established. They were however unaware of the extensive damage the larvae of the butterfly were doing to the geraniums and did not realize the species already had a strong foothold on the island.

Two weeks before the paper by Eitschberger & Stamer was published, Edward M. Raynor (1990) reported photographs of the lycaenid and identified it as "possibly *ethiopicus*" (one of the nine species belonging to the genus *Cacyreus*). And follows Raynor "As far as I'm aware, this genus has not been recorded from Europe or North Africa. Interestingly we observed further specimens in the nearby town of Magalluf, suggesting that the butterfly may be breeding on Majorca. Several members of this genus feed on geranium and pelargonium and they may have been introduced with plants,..". Raynor saw the butterfly for the first time in April 1990 when he was at a friends' garden in Cabo Falcó, south of Magalluf, and a bit later in Magalluf itself.

*Cacyreus marshalli* Butler, 1898 in Europe (31 August 1993)

✱   1-5    Records of very few specimens. Established breeding population not found

■   a-f    Established breeding population found.

Figure 1. Map of Western Europe showing where *Cacyreus marshalli* has been found so far (August 1993): 1* Cheshunt, Hertfordshire (United Kingdom) (1978), 2* Brussels (Belgium) (1991), 3* Castellón de la Plana (Spain) (1992), 4* Denia (Alicante-Spain) (April 1993), 5* Granada (Spain) (July 1993). In 1* to 5* only few specimens were found, with an established breeding population not detected. It is established on the islands of the Balearic archipelago (a) Ibiza, (b) Majorca and (c) Menorca. Breeding populations have also been recently found in July 1993 in (d) Logroño, (e) Zaragoza and (f) Valencia.

As to the two specimens collected near Castellón de la Plana, in Spain, it could not be assumed the species had already established itself on the Peninsula. To be certain it would be necessary to find a population of larvae on geraniums and check its permanence over time, as on Majorca. These two specimens, and perhaps others, might have been introduced
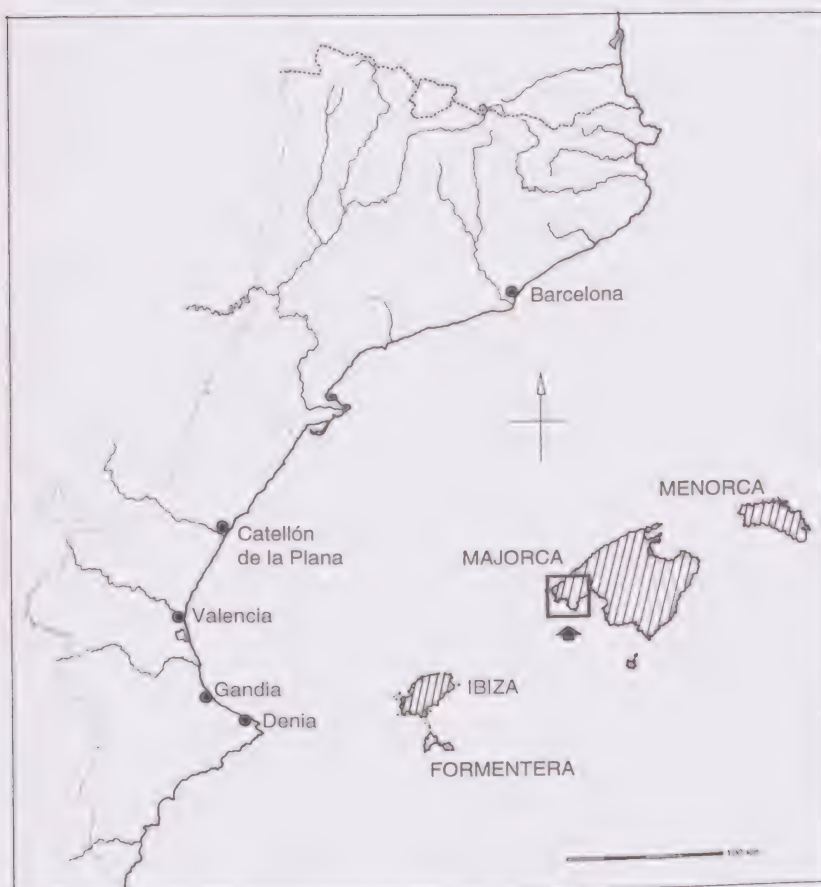
Figure 2. Map showing the territories of the Spanish Autonomous Communities of Catalonia, Valencia and Baleares. All major islands of the Balearic archipelago, with the exception of Formentera, are fully invaded by the pest. The square indicates the area where it is suspected *C. marshalli* took the first foothold on the archipelago.

from Majorca (it is known the species is not a migrant), probably as a larva or adult, and they would not have been able to establish a breeding population. The same would apply to the specimen found in Brussels.

Recently, I have been informed by my colleagues at the Plant Protection Service in the Autonomous Community of the Balearic islands that geranium growers settled on the island of Menorca, the second in size of the archipelago after Majorca, had detected this species inside their nurseries. Nearly simultaneously, a paper by the British entomologist P.R.Grey (1992) was published, where he reported the presence of the

species in gardens close to the sea located at Cala de Santa Galdana, on the south west of the island. The butterflies were detected in October 1991 and, on the occasion of a second visit of Grey to Menorca, again in early May 1992. Likewise, according to Grey, another lepidopterologist also found the species in April 1992, in Son Bou, village located on the south centre of the island. Thus, being aware of what happened to the island of Majorca, we can assume also the island of Menorca has been fully invaded by *Cacyreus marshalli*.

However, the Pityusic islands, Ibiza and Formentera, the closest to the Spanish mainland and the southernmost archilepagic islands, had so far not been reported as hosting *C. marshalli* populations. To check whether this species had established on these two islands, I visited Ibiza during December 27, 28 and 30, 1992, and Formentera, on December 29, 1992.

Results were positive on the island of Ibiza. Formentera seems to be, for the time being (December 1992), free of the pest.

On December 27, 1992 I found a large population of this pest in Sant Antoni de Portmany, a town located on the west coast of Ibiza. Geraniums were so infested, specially those in flowerpots near the harbour, that some young plants were completely dead. Older geraniums, within the same area, though alive, were severely damaged, with evident external and less obvious internal stem damage, the latter by galleries produced by boring larva inside the more tender upper stems. I found caterpillars in third and fourth (last) instars. These were found, healthy and active, feeding inside the galleries excavated in the stems. On the outside of the stems they produced the typical 'nibble' injuries (Sarto i Monteys, 1992). When entire stems were too damaged or, in the case of old geraniums, when only the tougher sections of the stems remained undamaged, then a few larvae were found feeding on leaves. I also found very healthy looking pupae and pupa exuviae attached external to the stems. However, I did not observe adults, probably due to the very low (for the area) December temperatures.

On December 30, 1992 the north of the island of Ibiza was explored, with two towns visited: Sant Miquel de Balansat (north centre) and Cala Sant Vicent (north east). The first is located inland, at a few kilometres from the coast and on hilly mountains; the second is by the sea. In both places I found *Cacyreus marshalli*, affecting both *Pelargonium zonale* and *Pelargonium peltatum*. At the first locality I found all larval instars. They were outside or inside terminal shoots which, together with the flower buds, are the preferred feeding sites. At the second locality only live pupae and pupa exuviae were detected, with damage produced on geraniums very obvious.

The temperatures on the island during these late December days were relatively low, with minima between 7 and 11°C. These temperatures seemed well tolerated by *C. marshalli* caterpillars. No photoperiod driven diapause (i.e. due to short daylength) was observed, contrary to what happens in most autochthonous lepidoptera. This had already been

observed by Sarto i Monteys & Masó (1991) in the laboratory during the winter months of December and January using a controlled and fixed temperature of 20°C. Their supposition appears supported that in the wild this species would not present a photoperiod-driven diapause and that low winter temperatures would simply slow down its biological cycle.

On the other hand, it seems the species has not yet reached the isle of Formentera. On December 29, 1992, I visited Formentera to search for this pest. It is the smallest regularly inhabited island of the balearic archipelago, with an area of only 100 km², and is southernmost in the group. A thorough search of geraniums was undertaken in all population centres as well as more isolated residential areas and country houses. In all locations geraniums were in excellent condition and neither the pest itself nor any vestige of its presence was detected. Occasionally, larvae of the noctuid moths *Heliothis armigera* (Hübner, [1808]) and *Chrysodeixis chalcites* (Esper, 1789) were found feeding on geranium leaves and flowers (the latter only on leaves).

Finally, in July 1993, established breeding populations, with large numbers, have been found thriving in continental Spain. These were detected in the cities of Logroño, Zaragoza and Valencia (see Figure 1).

## CONSIDERATIONS ABOUT ITS INTRODUCTION INTO THE BALEARIC ARCHIPELAGO

Another point to establish is when the introduction of this species into the islands of the balearic archipelago occurred, as it is not a migrant (Clark & Dickson, 1971; Eitschberger & Stamer, 1990). On Majorca, according to data provided by Mr. Joan Gomila and Mr. Antoni Cardona of the local Plant Protection Service, the first symptoms of geranium damage likely attributable to *C. marshalli*, were detected in 1987, within private gardens in Santa Ponça, town on the southwest of the island. The identity of the pest was unknown at that time. It follows that the most likely introduction occurred one or two years before.

In the case of of Ibiza, serious damage detected in some areas with the pest found in differing and widely separated localities, suggest that the whole island is invaded, indicating its introduction can not be too recent. It could have happened soon after its initial introduction in Majorca. And the same maybe true for the island of Menorca.

Recall that with low population levels damage to geraniums by *C. marshalli* is practically imperceptible. For an untrained person damage is easily mistaken with that produced by other larvae, such as the noctuid moth *Heliothis armigera*. The last species accounts for nearly 100% of all false alarms detected in Catalonia during actions undertaken to prevent the establishment of *C. marshalli* in this Autonomous Community. To a lesser extent the noctuid moth *Mamestra brassicae* (Linnaeus, 1758) is also involved. Both polyphagous species feed upon geranium flower buds and leaves, but do not affect the stems. Geranium leaves are eaten by a

number of polyphagous larvae, which in turn do not normally eat either flower buds or stems. These include the noctuid *Chrysodeixis chalcites* (Esper, 1789) and the tortricid *Cacoecimorpha pronubana* (Hübner, [1799]). All these species, though, are not geranium pests, with the damage produced small and generally undetected, and never killing the geraniums, which soon recover their healthy appearance. With *Cacyreus marshalli*, though, it is another matter.

It is likely that the southwest end of Majorca, which includes the towns of Paguera, Santa Ponça and Magalluf, was the area where the pest was first established, and from where it probably invaded the rest of the island. The data we have support this hypothesis: first symptoms of damage in Santa Ponça, first sightings of adults by Stamer in Paguera and by Raynor in Cabo Falcó and Magalluf.

I have collected and reared to adults around 300 *Cacyreus marshalli* immatures taken directly from the wild on Majorca. The specimens represent all stages from eggs to pupae, collected across different months and years, without producing a single parasitoid. Martin Honey obtained identical results with a smaller sample. This is very unusual result for autochthonous lycaenid species, which in the wild show parasitism rates of 20% to 30%, reaching in some cases 50%, as in *Iolana iolas* (Ochsenheimer, 1816) (López Munguira, pers. comm.)

This evidence indicates that to date no local autochthonous parasitoids of caterpillars have adapted to caterpillars of this alochthonous lepidoptera. Such an adaptation may happen over time. The lack of parasitoids would account for the population explosion of *Cacyreus marshalli*. In fact, this lycaenid has never been reported as a geranium pest in the countries where it is endemic (southern Africa), undoubtedly because there exist autochthonous parasitoids and predators which keep its population levels well below the pest threshold.

In view of the current colonisation of the three main Balearic islands it is no longer possible to establish with certainty which island received the original introduction of *C. marshalli*. However, the fact that the first symptoms were detected in 1987 on the island of Majorca, that the first collected specimens were taken on this island in mid-November 1989, and that three years later, the same story was repeated on Menorca and Ibiza, makes the hypothesis of its initial introduction into the island of Majorca most likely.

The coastlands of the Communities of Valencia and Catalonia, because of their closeness to the Balearic archipelago, are areas presenting the highest risk of pest introduction. However, two towns on the Valenciana coast present an even higher risk because they are regularly connected by ship to the Ibizan harbour of Sant Antoni de Portmany, where *C. marshalli* is very abundant. Denia in the province of Alicante and Gandia in the province of Valencia are both only about 110 km by sea from Ibiza. Given the high risk of introduction of *C. marshalli* into these localities, necessary preventative measures should be taken by competent authorities in the area.

## MEASURES TAKEN BY THE DIFFERENT ADMINISTRATIONS

The Community of Catalonia, through its Service of Plant Protection, started an information campaign in July 1992 by producing a poster and an information leaflet about the butterfly. The aims were to prevent the introduction of this pest into Catalonia and, should any focus be detected in Catalonia, to isolate it and impede its spread.

The Community of the Balearic Islands started a series of trials against this pest in June 1992, testing a total of six different insecticides. The results of these trials were positive, all tested chemicals controlled the pest, with no significant differences among them. Treatments will continue during 1993 (J. Gomila, pers.comm.).

In addition the EPPO (European and Mediterranean Plant Protection Organization), to which Spain belongs, showed concern about this pest in Europe and took the first steps to determine whether or not it was appropiate to declare a quarantine status for this species in Europe in May 1992. Its final decision is pending.

## COMMENTS ON THE ECONOMIC IMPORTANCE OF GERANIUMS AND POSSIBILITIES OF CONTROL OF THE PEST

In the Spanish national ranking of ornamental plants, geraniums (i.e. all cultivated varieties of the genus *Pelargonium*) are by far the most important in sales volume as well as in employment for production and marketing. Today there are in continental Spain four major geranium growers, who produce 10 million cuttings a year, distributed to about 500 nursery owners across Spain. Altogether this represents a market of over $30 million a year.

The United States and Germany are presently the two leading countries in the production and commercialization of geraniums, with 23% and 16% respectively of the world production, estimated at 500 million geraniums a year. In the U.S.A. the wholesale value of geraniums in 1990 exceeded $160 million, representing 17.3% of all U.S. wholesale bedding plant sales (Berninger, 1992).

As cited above, the last surveys in the balearic archipelago showed that practically all geraniums on the islands of Majorca, Menorca and Ibiza are affected by the pest. People owning gardens, especially those of restaurants with gardens important in creating atmosphere, have already started to substitute geraniums with other species of plants, to the detriment of the geranium industry.

Falling sales of the Spanish wholesale growers are already noticeable. According to data provided by 'Cultius Roig', one of the four major growers mentioned above, with headquarters in Catalonia, the number of geranium cuttings despatched to the island of Majorca fell from 78.582 during the 1991-1992 season to 60.471 during that of 1992-1993 (seasons extend from September to March), a 23% decrease. It is not surprising that growers are concerned about spreading of this pest.

Control of *C. marshalli* in geranium nurseries should not be a problem with precautionary insecticide controls carried out regularly.

The control problem is outside the nurseries after the geranium reaches the consumer as a consequence of the biology of the butterfly. This results from the two first larval instars being obligate endophytes while the last two are facultative endophytes (Sarto i Monteys, 1992). Accordingly contact insecticides (most insecticides) will be useful against the non-endophytic phases, but useless against the endophytic phases which are inside the geranium stems and flowers away from insecticide action. Systemic insecticides, i.e. those penetrating inside plant tissues, would be efficient. However, because of their high toxicity, many are not advisable for domestic gardening.

Another worry concerns the possible adaptation of *C. marshalli* to autochthonous species of wild geraniums of the genus *Geranium*, which has already been confirmed with some species in the laboratory (Sarto i Monteys, 1992). The natural foodplant of the butterfly belong to the genera *Geranium* and *Pelargonium* (Clark & Dickson, 1971). If adaptation to wild species occurred, eradication of *C. marshalli* would be practically impossible as there will always exist the risk of reinfestation from wild geraniums.

The most rational alternative would be biological control by its natural parasitoids, to be obtained in the area from which it naturally occurs. Those might accomplish in a short time a much more efficient and cleaner control than that given by chemical insecticides.

In summary, if this pest invaded the Iberian Peninsula or other mediterranean areas from its base on the balearic archipelago, it could

---

Color Plate 1 (Facing Page)

Figure    1. *Cacyreus marshalli* adult (upperside)
         2. *Cacyreus marshalli* adult (underside)
         3. Hatched egg on geranium sepal
         4. Endophytic phase: first instar larva and early damage on geranium flower (The cavity has been opened to show larva)
         5. *C. marshalli* pupa
         6. Endophytic phase: second instar larva boring inside a geranium inforescence peduncle. The gallery has been opened to show larva and its damage. The dark segment above the larva corresponds to its excreta.
         7. Exophytic phase: fourth instar larva feeding from outside on a geranium flower. Notice the larva has its first third inside the young flower, after it pierced the flower sepals to access it.
         8. Exophytic phase: fourth instar larva "nibbling" a geranium stem from outside.
         9. Damage on geranium flowers, pedicels and inflorescence peduncle.
         10. Damage on geranium stem. Stem emptied by *C. marshalli* endophytic activity. The interior gallery has been partially opened to show damage. Notice it is fully filled up with larval excreta.

potentially damage all economic activity committed to the production and commercialization of geraniums. Its partially endophytic habits and its possible adaptation to wild autochthonous geraniums, make the long term consequences difficult to predict.

## LITERATURE CITED

BERNINGER, L.M. 1992. Status of the Industry. In J.W. White. Geraniums IV: 412 pp. Ball Publishing. Geneva (Illinois).

CLARK, G.C. & C.G.C. DICKSON. 1971. Life Histories of the South African Lycaenid Butterflies. 270 pp. Purnell. Cape Town.

EITSCHBERGER, U. & P. STAMER. 1990. *Cacyreus marshalli* Butler, 1898, eine neue Tagfalterart für sie europäische Fauna? (Lepidoptera, Lycaenidae). Atalanta, 21(1/2): 101-108.

GREY, P.R. 1992. The occurrence of *Cacyreus marshalli* (Lycaenidae) in Menorca. Butterfly Conservation News, 52: 8-9.

MASÓ, A. & V. SARTO I MONTEYS. 1991. Una mariposa amenaza los geranios europeos. La Vanguardia. Supl. de Ciencia y Tecnología: 9.

RAYNOR, E.M. 1990. The occurrence of a *Cacyreus* species (Lep.: Lycaenidae) in Majorca. Entomologist's Record, 102: 250.

SARTO I MONTEYS, V. 1992. El taladro de los geranios. *Cacyreus marshalli*, grave plaga de los geranios europeos: su biología, síntomas y daños. Horticultura, 83: 13-19.

——. 1993. Primer hallazgo en el continente europeo de puestas del licénido sudafricano *Cacyneas marshalli* Butler, 1898 (Lep. Lycaenidae. Shilap Revta. lepid., 21(83): 191-197.

SARTO I MONTEYS, V. & A. MASÓ. 1991. Confirmación de *Cacyreus marshalli* Butler, 1898 (Lycaenidae, Polyommatinae) como nueva especie para la fauna europea. Bol. San. Veg. Plagas, 17: 173-183.

# Why Are There So Few Butterflies In The High Andes?

Arthur M. Shapiro

Center for Population Biology, University of California, Davis, CA 95616

**Abstract**. The high Andes have a depauperate butterfly fauna even though they are adjacent to the faunistically rich Amazonian lowlands. Andean oreal butterfly faunas are impoverished even as compared to the mountains of California. There is a tradition of attributing the high-Andean fauna to Holarctic lineages which colonized South America in the Great American Interchange some 2-3 million years ago. Most of the critical taxonomic relationships are too poorly resolved to separate common ancestry from convergence, but in at least the Thecline Lycaenids cladistic studies strongly support convergence. Unusual aspects of the Andean and Patagonian butterfly faunas (including relationships between the tropical Andes and the temperate south, host-plant relationships, and the dominant position of the Pronophiline Satyrids) are reviewed and placed in both biogeographic and paleogeographic contexts.

The richness of lowland Neotropical butterfly faunas is proverbial. The famous latitudinal gradient in biodiversity is not, however, repeated in the butterflies of very high altitudes in the Neotropics. As a result, the latitudinal gradient in biodiversity is oversteepened in the New World tropics relative to temperate latitudes. Equatorial Andean butterfly faunas are both absolutely and relatively impoverished in comparison to both temperate oreal (high-mountain) faunas and adjacent lowland ones. Why should this be so?

The diversity of any high-altitude biota should in theory be related to at least the following factors: (i) the antiquity of the environments in question, (ii) the availability of preadapted biota to colonize them in ecological time, (iii) the availability of sources of potential colonizers which could adapt to oreal conditions in evolutionary time, and (iv) the area of the environments (in terms of species-area relationships).

The oreal butterflies of the Andes and the Sierra Nevada of California, the great mountain ranges of the far west of South and North America respectively, may be compared instructively from a biogeographical standpoint. The comparison is not, however, without problems. Both are generally considered young mountain ranges, achieving their present heights and first presenting the opportunity for the development of an oreal biota in Plio-Pleistocene time. [Molnar and England (1990) have challenged this conventional wisdom. Their position, if correct, would force the re-evaluation of virtually all existing scenarios in montane-oreal biogeography. For purposes of this paper, the conventional assumptions about the ages of the Andes and Sierra Nevada will be accepted.] In

both ranges, the emergence of alpine environments coincided temporally with the climatic instability of the Pleistocene, with its repeated episodes of glaciation. The climatic and vegetational histories of both in the Quaternary are fairly well documented, though the record for both the northern Andes (work of Van der Hammen and Cleef) and the far south (Patagonia and Fuegia; work of Auer, Mercer and others) (see references in Shapiro, 1991a) is denser, more continuous, and in general more satisfactory than what is currently available for the Sierra Nevada (Heusser and King, 1988; Fullerton, 1986). A very detailed picture is emerging for the late Quaternary of forested, humid Chile (Ashworth and Hoganson, 1993) which is unfortunately not very useful for butterflies, since the butterfly fauna of these climates is so poor.

Area comparisons are difficult. The Andes are not a single mountain chain, but a huge complex extending from 10° N to 54° S Latitude, incorporating a vast area of high plateaux, the Peruvian-Bolivian *altipl- ano*. The northern Andes are often humid or at least seasonally so; farther south occur various semiarid to extreme desertic regimes, and still farther south the cool-temperate rain forests of archipelagic Chile. The Sierra Nevada is much more modest in scale. Although it is some- times considered the world's longest single continuous mountain chain, it demonstrates little north-south climatic differentiation in comparison to the Andes — but then, it is confined within a latitudinal range from 40° to 36° N. Climatically, the oreal Sierra Nevada is most directly compa- rable to the corresponding sector at the latitude of Mendoza, Argentina, south to northernmost Patagonia (33-44° S). At these latitudes the Andes separate the Mediterranean climate of the Chilean Central Valley from the more continental climate of the Argentine *monte* (high desert), just as the Sierra stands between the Mediterranean climate of the California Central Valley and the continental desertic or subdesertic climate of the Great Basin in Nevada. A better latitudinal comparison would include the North American Cascades, Coast Ranges, and some of the Alaskan mountains, but detailed butterfly faunistic information was not avail- able for this purpose. The relationship of the Mexican montane (virtually no oreal) butterfly faunas to those of the lowland tropics is complex enough to warrant entirely separate consideration.

The high altitudes of the Andes embrace a variety of oreal vegetation formations, variously called *páramo* (humid to semiarid) in the north,

---

Plate I.   Upper left: South Andean - Patagonian small fritillaries (*Yramea*) (top two rows) and their Boreal counterparts (*Clossiana*). Both groups feed on Violaceae and Rosaceae, but is this indicative of relatedness or merely another level of convergence? Upper right: Undescribed *Yramea* (near *inca*) from northwestern Argentina, showing male "green" melanization convergent to sympatric *Colias blameyi* and to the Boreal *Clossiana improba*. Lower: upper- and undersides of male *Baltia* from Gyaco La, Tibet (5250m) (above) and *Phulia* from Cordón del Viento, Argentina (3700m).

*jalca* (humid or subhumid) in Peru, and *puna* and *altiplano* (mostly semiarid to arid) in Peru, Bolivia, Chile and Argentina. In the Southern Cone the oreal belt dips ever lower as one progresses south, and south-end-of-the-world taxa become increasingly prominent in the flora. The Andean oreal communities differ tremendously in floristics, faunistics, aspect and seasonality, though a surprising number of plant and animal genera span much of this latitudinal diversity. By contrast, the Sierra Nevada oreal zone is relatively uniform, with a gentle north-south climatic gradient; the most dramatic floristic (and butterfly-faunistic) differences are often defined edaphically rather than latitudinally.

Defining the oreal zone is somewhat arbitrary in those parts of the Andes (as well as in the eastern Sierra Nevada) where there is no "tree line" because there are no trees. In parts of the northern Andes, more-over, deforestation has led to a downslope migration by *páramo* vegeta-tion into land formerly occupied by the upper cloud forest. Any quantita-tive analysis of species-area relationships must also correct the area of oreal communities for the degrees of latitude spanned, and perhaps for other things. All these complications raise doubts about pursuing this approach; the trend, in any case, is obvious and unlikely to be greatly elaborated by such analyses.

The matter of source regions for potential colonizers is critical for our comparison. The Andes directly adjoin the world's greatest center of biodiversity — Amazonia — and one normally assumes that the lowland habitats and communities are older than their highland neighbors: Amazonia is thus the most obvious source for potential high-altitude colonizers, and the butterfly diversity of Amazonia is the world's highest. Butterfly diversity in areas near the Sierra Nevada and likely to contrib-ute to its oreal fauna is an order of magnitude lower. By the time the Sierra had reached alpine heights, access to the humid-neotropical Tertiary biota had been shut off. Indeed, the rise of the Sierra itself administered the *coup de grâce* by altering the rainfall patterns in ways hostile to that biota. Any emerging Sierran oreal biota would henceforth be recruited from what may be broadly characterized as Madro-Tertiary and Arcto-Tertiary sources. (These terms are used loosely, since recent paleovegetational scenarios, e.g., Wolfe, 1985, are considerably more complex than the classic formulation by Axelrod.) At any rate, if we assume that all lowland lineages have an equal initial probability of colonizing the oreal zone (obviously untrue), many more lineages are available to the tropical Andes than to the Sierra Nevada. *Ceteris paribus*, there should be much more butterfly diversity in the tropical than the Sierran oreal zone. And there is not.

If we consider just ecological time, species preadapted to the physiologi-cal rigor of life in the oreal zone might be assumed to be more readily available to the Sierra Nevada. However, this is not absolutely certain. Mercer and Sutter (1982) and Clapperton (1983) suggest that glaciation began in southern Patagonia some seven million years ago, more or less

contemporaneously with the first hints in Alaska. Thus, a cold-adapted butterfly fauna could have existed in the far south of South America, moving north up the spine of the Andes like the Austral flora. However, this presupposes the existence of any Austral butterfly fauna that far back. If there was a Patagonian butterfly fauna, it must have been very undiverse. (There is no paleontological or convincing biogeographic evidence for the existence of an Austral butterfly fauna prior to the breakup of Gondwanaland.) In the large and diversified Laurasian land mass, butterflies would have had much more opportunity to adapt to continental climates than in the Southern Cone of South America; both Arcto- and Madro-Tertiary species might be expected to be better adapted to emerging oreal conditions than lowland tropical ones would be, as discussed later.

## How Good are the Data?

There is no Andean oreal butterfly fauna that can be considered truly well-known. This is particularly true of the tropical Andes, where most collecting has been done by transient visitors in an unsystematic way, at random and often inappropriate seasons. The seasonal component of butterfly diversity is very poorly understood in the high Andes. Most of the collecting has been done along trans-Andean highways, and therefore emphasizes the faunas of plant communities found in and near passes. Many habitats have never been collected at all. Thus all the Andean data must be considered provisional. The only attempt to date to collate such information is Descimon's (1986), using in part the antique data of Fassl (various publications cited in Descimon, *loc. cit.*) as well as his own field experience. Descimon tabulates "oreal faunas" from the Sierra Nevada de Santa Marta in the far north (Colombia) to southern Tierra del Fuego, ranging from two (Santa Marta) to 35 ("S Peru") species. There is at least a crude suggestion of a double cline of species richness here, which cannot be rationalized by latitude but might be on other grounds. However, the data are very unreliable. The largest faunas are large-scale territorial composites ("S Peru," "Bolivia") while the smallest (Santa Marta, Cordillera de Mérida, Tierra del Fuego) are much smaller in both extent and ecological diversity. (The Sierra Nevada de Santa Marta is actually not even part of the Andes.) The definition of "oreal" here is also disturbingly vague. There are no butterflies in the oreal zone in southern Patagonia and Fuegia, if that zone is defined as being above the tree line. (Two species — *Yramea cytheris* and *Hyposchila microdice* — make it just to tree line in the Cordillera Martial behind Ushuaia.) The Patagonian fauna enumerated by Descimon (eight species) does not match any Patagonian fauna I have seen. It omits the rich Satyrid fauna (surprisingly, since this fauna has been monographed), the unexpectedly speciose hairstreaks (not surprisingly omitted since most of the species were still undescribed in 1986, and many still may be), and the blues, but includes *Colias lesbia*, which is resident only along the Gulf

of San Jorge in the south; yet it leaves out *Tatochila autodice* and *T. vanvolxemii*, whose Patagonian ranges match that of *C. lesbia*. And the Sierra Nevada de Santa Marta fauna omits 50 percent of the recorded butterfly species (*Reliquia santamarta*, referred to elsewhere in Descimon's paper!, and an at-that-time unnamed hairstreak). And all of the faunas omit the Hesperiidae altogether.

These are definitional problems, oversights, or results of lack of communication. There is a more profound problem underlying any such analyses, however, and that is sheer ignorance. Even in the temperate Argentine Andes, the alpine faunas cannot be considered well-known. The biogeographically important species *Colias mendozina* was collected twice near the turn of the century and then lost until 1989, when I rediscovered it — ten minutes' walk from the transandean superhighway connecting Argentina and Chile at Las Cuevas! The Lycaenid fauna of the same area (the Aconcagua Provincial Park, collected — albeit sporadically — for over a century) was largely undescribed before 1992. Slightly farther north, the "Chilean endemic" *Colias flaveola* was just discovered in 1988 living happily on the Argentine side of the crest in the Province of San Juan. If this sort of thing is routine in the best-collected and most accessible Andean oreal fauna, what must be true farther north? Although a Lycaenid sibling species new to science has just been recognized in the Sierra Nevada oreal fauna (J.F. Emmel, pers. comm.), the overall situation is clearly much better in California than in the Andes. Thirty years ago little of the high country had been collected and many common, widespread oreal species were thought of as rare and very localized. Now, however, there has been plenty of collecting in midsummer near the accessible passes, and a respectable amount in more remote areas. The beginning and end of the season are less well-documented, although it is unlikely any more new species are to be found then (for the same reason as collectors rarely venture in at such seasons: the weather is too unpredictable for butterflies to count on flying then). Some Sierran oreal areas become snowfree in spring before the forested regions below, and are accessible only on skis or snowshoes during the first few weeks of the flight season. Because many species emerge quickly after snowmelt, this renders our phenological data at least less than ideal. It is, however, safe to say that the broad outlines of Sierran butterfly faunistics are now well-defined and major surprises are unlikely.

---

Plate II. Above: Holarctic (left) and South Andean - Patagonian (right) Satyridae of steppe and tundra habitats. All the South American taxa are Pronophilini; the Holarctic ones are Maniolini and Erebiini. Below: Repeated evolution of "green" *Colias* phenotypes in cold climates. Each pair represents a different sublineage, and the non-green specimen is the postulated closest relative of the greens; all are males. Top: *C. behrii* (California) and *C. palaeno* (circumpolar). Center: *C. nastes* and *C. hecla* (both Alaska). Bottom: *C. weberbaueri* and *C. euxanthe* (Bolivia).

In selecting sites for comparison, both Andean and Sierran, I have emphasized accessibility and completeness of coverage. The data (Tables 1, 2) are striking — just as striking, in fact, as Descimon's. It is almost certainly biologically significant that all of the northern Californian oreal faunas are richer than any of the Andean ones, which run from 10° N (Sierra Nevada de Santa Marta) to the temperate Paso Bermejo at the Aconcagua Provincial Park (33° S). Moreover, the impoverishment in species in the Andean faunas is mirrored by their impoverishment in lineages; it is unlikely that other groups will duplicate the recently-discovered richness of the Lycaenid fauna discussed below, because among the butterflies the Lycaenids seem uniquely prone to philopatry, intense host specialization, and cryptic speciation.

## ORIGINS OF THE SIERRAN OREAL FAUNA

In a very important paper, Chabot and Billings (1972) demonstrated that the largest contributor to the constitution of the Sierran oreal flora was the Great Basin. This is a flora already adapted to intense winter cold, intense insolation, and a general water deficit year-round, albeit with summer rain. A substantial number of plant species, such as Bitterbrush (*Purshia tridentata*, Rosaceae), Sagebrush (*Artemisia* spp., Compositae), and Daggerpod (*Phoenicaulis cheiranthoides*, Cruciferae) are equally at home in high desert and at tree line. The same is true of several butterflies, such as *Lycaena heteronea*, *Euphilotes battoides*, *Satyrium fuliginosum*, *Lycaeides melissa* (all Lycaenidae) and *Pontia occidentalis* (Pieridae). (Of these, *L. melissa* alone is suspected of being more than one genetic species.) The Sierra has the smallest percentage of circumpolar relict plants in its oreal flora of any northern-hemisphere mountain range so far from the Equator. Pleistocene conditions undoubtedly shaped the access of such elements (represented conspicuously by Mountain Sorrel, *Oxyria digyna*, Polygonaceae) to the Sierra. They could have come from the north, northeast or east (across the Great Basin from the Rockies, see below; the "Convict Creek flora" of Major and Bamberg, 1967 is the classic argument for cross-Basin dispersal, subsequently reinforced by studies of pack rat middens (Betancourt et al. 1990)).

Most butterfly taxa of the Sierran oreal zone are conspecific with Rocky Mountain taxa, and the subspeciation in most cases is weak. The Rocky Mountain fauna has been attenuated by distance, but also by extinctions in the Xerothermic (Hypsithermal). During this warm interval a few thousand years ago, cold-adapted organisms were driven to extinction in the low northern Sierra north of Donner Pass, resulting in disjunctions between the northwest California (Klamath-Trinity-Siskiyou-Eddy) and central and southern Sierra oreal zones. The most famous of these is Foxtail Pine, *Pinus balfouriana*. The most important Rocky Mountain oreal element conspicuously missing from the Sierran fauna is the genus *Erebia* (Satyridae). Moreover, the taxonomic distance between the Sierran oreal butterfly fauna and the adjacent low-elevation faunas is not

Table 1. Oreal Butterfly Faunal Composition

| | Trinity Alps[a] | Mt. Eddy[a] | Castle Peak[b] | Carson Pass[c] | Yosemite[d] |
|---|---|---|---|---|---|
| Satyridae | 0 | 0 | 2 | 3 | 2 |
| Nymphalidae | 12 | 11 | 10 | 19 | 13 |
| Lycaenidae | | | | | |
| Theclinae | 3 | 2 | 4 | 6 | 2 |
| Lycaeninae | 3 | 3 | 5 | 5 | 7 |
| Plebeiinae | 9 | 9 | 9 | 14 | 10 |
| Riodinidae | 1 | 1 | 0 | 0 | 0 |
| Pieridae | | | | | |
| Euchloinae | 2 | 1 | 3 | 2 | 1 |
| Coliadinae | 1 | 1 | 1 | 1 | 2 |
| Pierinae | 2 | 2 | 2 | 2 | 2 |
| Papilionidae | 4 | 4 | 4 | 5 | 4 |
| Hesperiidae | | | | | |
| Pyrginae | 2 | 2 | 4 | 3 | 1 |
| Hesperiinae | 4 | 4 | 4 | 4 | 5 |
| Totals | 43 | 40 | 48 | 64 | 49 |

| | Sierra Nevada de Sta. Marta[e] | Morococha-Ticlio[f] | Cumbres Calchaquíes[g] | Paso Bermejo[h] |
|---|---|---|---|---|
| Satyridae | 0 | 2 | 5 | 5 |
| Nymphalidae | 0 | 2 | 5 | 4 |
| Lycaenidae | | | | |
| Theclinae | 1 | 3 | 4 | 3 |
| Plebeiinae | 0 | 1 | 3 | 3 |
| Pieridae | | | | |
| Coliadinae | 0 | 3 | 3 | 2 |
| Pierinae | 2 | 5 | 8 | 3 |
| Hesperiidae | | | | |
| Pyrginae | 0 | 2 | 2 | 1 |
| Hesperiinae | 1 | 3 | 3 | 0 |
| Totals | 4 | 22 | 33 | 21 |

Notes: Strictly migratory or casual spp. omitted from all tallies. [a]Shapiro, Palm & Wcislo 1981. [b]Shapiro 1978 + unpublished. [c]Shapiro, unpubl. data 1972-90. [d]Garth & Tilden, 1963 + unpublished from various sources. [e]Colombia, Dept. Cesar, above 3500m. [f]Peru, Dpto. Junín, above 4400m. [g]Argentina, Prov. Tucumán, above 3000m. [h]Argentina, Prov. Mendoza, above 2700m. [e-h]Shapiro, unpublished data + data from other sources.

Table 2. General characteristics of oreal butterfly faunas in North and South America and their regional affinities.

| Some Important Andean Oreal Butterfly Genera | | | |
|---|---|---|---|
| | In Holarctic oreal? | In lowland Neotropics? | In Patagonia? |
| Hesperiidae | | | |
| *Pyrgus* | Yes | Yes | Yes |
| *Hylephila* (*boulettii* group) | No | Yes | Yes |
| Pieridae | | | |
| *Colias* | Yes | No | Yes |
| *Tatochila* | No | No | Yes |
| *Hypsochila* | No | No | Yes |
| *Phulia* | No, but cf. *Baltia* | No | No |
| *Pierphulia* | No | No | No |
| *Piercolias* | No | No | No |
| *Infraphulia* | No | No | No |
| *Reliquia* | No | No | No |
| Lycaenidae | | | |
| *"Itylos"* sensu lato | No | No | Yes |
| *Eiseliana* | No | No | No |
| *Penaincisalia* | No | No | Yes |
| Nymphalidae | | | |
| *Yramea* | No, but cf. *Boloria* | No | Yes |
| *Vanessa* (seasonal migrants?) | Yes | Yes | Yes |
| Satyridae | | | |
| (various Pronophilini) | Entire tribe absent | Yes | Yes |

| Some Important Sierran Oreal Butterfly Genera | | | |
|---|---|---|---|
| | In Andean Region? | In Great Basin? | In Rocky Mountain Oreal? |
| Hesperiidae | | | |
| *Pyrgus* | Yes | Yes | Yes |
| *Hesperia* | No | Yes | Yes |
| Pieridae | | | |
| *Pontia* | No | Yes | Yes |
| *Colias* | Yes | Yes | Yes |
| Lycaenidae | | | |
| *Lycaena* | No | Yes | Yes |
| *Agriades* | No | Yes | Yes |
| *Lycaeides* | No | Yes | Yes |
| Nymphalidae | | | |
| *Boloria* + *Brenthis* | No, but cf. *Yramea* | (Yes)[a] | Yes |
| Satyridae | | | |
| *Oeneis* | No | Yes | Yes |
| *Neominois* | No | Yes | (Yes)[b] |

Notes: [a]Only in montane habitats. [b]Present mostly below the oreal zone in the Rockies.

striking. All of the oreal species have lower-elevation congeners nearby (except *Neominois* which only goes lower much farther east), and a rather large number of oreal species extend some distance below tree line as well. There is none of the sense, described by Descimon for the Andes, of entering a different world when one passes from the montane to the oreal fauna.

The oreal butterflies of far northern California (which has only tiny areas of climatically treeless highlands) are a southward extension of the Cascadian fauna. They are much less like the Rocky Mountain fauna than is the Sierran one. The oreal-endemic Sierran *Oeneis* (*ivallda* and *stanislaus*) present the strongest case for cross-Basin dispersal (Porter and Shapiro, 1990). To the contrary, the Fritillary *Speyeria mormonia* connects up its Cascadian and Sierran subspecies via a series of small, relict populations (Mount Eddy, Ball Mountain, Warner Mountains) which constitute our best butterfly evidence so far of a northerly access route, though by no means conclusive.

Although North America acquired some butterfly taxa in the Great American Interchange of flora and fauna which commenced some three million years ago (Stehli and Webb, 1985; Simpson, 1980), the impact on the Sierran alpine butterfly fauna was nil; specifically, no Andean butterflies appear to have colonized the Sierra. One Andean butterfly (*Nathalis iole*, which is a montane or oreal species in Colombia, not noted by Descimon) did successfully occupy North America — but in desert, montane and warm-temperate, not oreal communities. Only one Sierran oreal species (*Thorybes mexicana* ssp.) is even of Madro-Tertiary provenance! Otherwise, the Sierran oreal fauna is ultimately all Arcto-Tertiary or derivative therefrom.

The genus *Pyrgus* (Hesperiidae) is of special interest because it has speciated in the Andes and Patagonia to a greater extent than in North America, and several of its species are oreal. No phylogenetic analysis of *Pyrgus* has been done, but superficially it does not appear that there has been any communication in either direction between the western North American and the Andean oreal *Pyrgus* faunae. The large Andean Hesperiid genus *Hylephila*, with several important oreal taxa from the Sierra Nevada de Santa Marta to Patagonia, apparently entered lowland North America as the subtropical weedy species *H. phyleus* in or after the Great American Interchange, but never penetrated the mountains.

## Origins of the Andean Oreal Fauna

The Andean oreal faunas are derived from a remarkably small number of lineages, probably fewer than 20, most of which have been attributed by most authorities to invasion from the north at the time of the Great American Interchange. If this notion is correct, the imbalance is very striking: northern invaders allegedly defined the entire Andean oreal fauna, while southern ones had zero impact in the Sierra Nevada.

The notion of a northern origin for the Andean oreal fauna originated in the 19th Century. Initially many Andean species were described in Palearctic genera, based on superficial, but often strong, resemblances in habitus. Eurocentrism and a subsequent analogy between the migrations of *Homo sapiens* and the supposed migrations of butterflies in geologic time colored subsequent phylogenetic speculation. Dixey (1894, pp. 322-326), for example, wrote:

> In the Chilian or Andesian division of the Neotropical Region we find the genus *Tatochila*, which appears not to belong to the regular Neotropical Pierine stock, but to be closely related to the Palearctic *Pontias*. It is conceivable that the latter stem may have spread from Asia into the western portion of the Nearctic continent, and thence down the mountain chains to the south... Another indication of the same invasion is afforded by the genus *Phulia*, now found with the nearly-allied *Tatochila* only in the Andesian or Chilian Subregion, to which it no doubt made its way along the great mountain chains in a similar manner. Its close ally *Baltia* remains in the high lands of Central Asia, where it bears much the same relation to *Synchloe* as *Phulia* to *Tatochila*... The earliest species of *Synchloe* were undoubtedly differentiated from *Pontia* or *Baltia* in the Palearctic Region, from which the genus spread (probably eastwards) into the Nearctic.

This is in keeping with the attitude reflected in a famous quote from Wallace (1876):

> The north and south division of the modern biota represents the fact that the great northern continents are the seat and birthplace of all the higher forms of life, while the southern continents have derived the greater part, if not the whole, of their vertebrate fauna from the north...

Dixey's scenario was repeated by Klots (1932), Mani (1968), and even Descimon (1986, p. 526), who wrote:

> In summary, it is clear that the Neotropical and southern temperate regions contributed little (or nothing) to the oreal butterfly fauna of the Andes. Its affinities lie instead with the Holarctic realm.

This is certainly in keeping with the traditional viewpoint of plant geographers, who noted early the conspicuous predominance of Holarctic plant lineages above the Andean tree line. Such genera as *Castilleja* (Scrophulariaceae) and *Lupinus* (Leguminosae) are conspicuous elements in the northern Andean *páramos*; they are clearly of northern provenance and diminish in importance southward, as one would expect if they were fairly recent arrivals. With striking symmetry, most of the lowland plant diversity — and with it, most lowland tropical plant lineages — disappears at tree line. The turnover in floristics was attributed by Walter and Medina (1969) to the difficulty in acclimating evolutionarily to the diel thermal regime in the *páramo* — with daily

maxima as high as 15-20 °C but nightly minima below freezing most nights of the year.

If the Andean oreal regime arose at about the same time as the Great American Interchange, it can be argued, Holarctic cold-adapted plants travelling by sweepstakes dispersal would probably arrive before many lowland-tropical plants could have adapted to highland conditions. These plants, and the cool-adapted Austral flora migrating north from Valdivia, would then have competitively locked up the oreal zone and prevented much penetration from the lowland floras. In turn, the Holarctic butterflies, preadapted to feed on Holarctic plants, would have followed them south. The lowland butterfly fauna, with no coevolutionary history of dealing with Holarctic plants and their phytochemistry, would have been deterred if not excluded from the highlands. This is essentially Descimon's scenario. It is in the great tradition of narrative biogeography: seductive, plausible, and difficult to falsify. Descimon's argument has been falsified for one lineage, the hairstreaks (Theclini or Eumaeini, Lycaenidae). Kurt Johnson and his collaborators have shown that the various high-Andean and Patagonian hairstreaks, mostly undescribed or known from very few specimens, and treated by most workers including Descimon as of Holarctic affinities, are merely convergent in phenotype to Holarctic hairstreaks (Johnson 1991a,b; Johnson, Miller & Herrera 1992). They really are derived from the lowland-tropical hairstreak fauna. This is true of both the "Andean *Incisalia*" and the characteristic genus *Eiseliana* of the Argentine *puna*. Furthermore, most of the hairstreak genera represented in the high-Andean fauna have congeners in Patagonia, and most are richer in the south than in the north. One of Johnson's new genera has species from oreal Colombia to the Argentine province of Chubut. (This repeating pattern is the same as that seen in the Pronophiline Satyrids, discussed further below.)

Are any other components of the oreal fauna likely to be re-evaluated in this way? There has been an explosion of interest in the Andean blues (Lycaenidae, Polyommatini) resulting in unfortunate taxonomic confusion (Balletto, 1993; Bálint and Johnson 1993a,b; Bálint 1993). Their greatest richness is in northern and central Argentina, Bolivia and Chile. The work of these authors has demonstrated convincingly that the previous appearance of low diversity in these blues was illusory. The ranges of most of the newly-recognized species are very poorly known, and it is not obvious whether geographic or ecological replacement, seasonal allochrony, or sympatry and synchrony properly define the structure of all this richness. Nor has the phylogenetic position of the Andean fauna — along with its geographic relationships — yet been defined. To do so is urgent, especially vis-à-vis the Asian oreal and steppe fauna.

Meanwhile, Lee Miller (pers. comm.) has revised his opinion of the Pronophilini, incorporated by Descimon in his scenario. Miller now believes that the family Satyridae is of Gondwanian origin (no later than

early Cretaceous, obviously) and only entered the Northern Hemisphere by riding India into the underbelly of Laurasia. By this scenario, the Pronophilines are primitively autochthonous in South America. When we recall that the oldest butterfly fossils are only Oligocene, it is evident that the days of extreme conservatism in blaming everything on the Pleistocene and the Great American Interchange are over. The danger now is of over-reaction — of projecting butterfly evolution back into the Devonian, if not the Pre-Cambrian.

## FURTHER CONSIDERATION OF THE PIERIDAE

Descimon focuses especially on the Pierini and the genus *Colias*. Let us consider *Colias* first. Again, our modern scenario reflects Dixey, 1894 (pp. 326-327):

> No other genus in the whole subfamily has so extensive a range as *Colias*... Here again, I have little doubt that the site of original divergence is Asiatic... after populating the Palearctic and Nearctic continents with numerous species [it has] passed down the great mountain chains of Central and South America to Chili and Patagonia, and has even established outposts in Venezuela and the Sandwich Islands (the occurrence of *Colias* in the last-named locality is, however, not entirely free from doubt).

All taxonomists but Berger (1988) have treated the Andean *Colias* implicitly as a monophyletic group, displaying little morphological change but great adaptive radiation in color, pattern and sexual dimorphism which more or less duplicates what occurs elsewhere in the world. (There has been no global cladistic analysis of *Colias* — perhaps surprisingly.) *Colias* is overwhelmingly a Holarctic genus, with greatest diversity in Asia both in terms of species and species-groups. Hardly any *Colias* occur in forests; they are steppe insects *par excellence* and their current distribution in the Holarctic shows the influence of the periglacial steppe-tundra. Most of the species whose life-histories are known feed on Papilionaceous legumes, especially *Vicia*, *Lathyrus*, *Trifolium*, *Astragalus* and related genera. In the Holarctic there are small groups of willow-(Salicaceae) and Ericaceae-feeding species (more diverse in the Nearctic than in the Palearctic). The southernmost Ericad feeder, *C. behrii*, is endemic to the central and southern Sierra Nevada, probably of Pleistocene origin and derivative of *C. palaeno* (or perhaps *C. pelidne*).

The Andean *Colias* reared to date are all Papilionaceous-Legume feeders. Most of them now routinely breed on naturalized clover (*Trifolium repens*) and/or alfalfa (*Medicago sativa*) and in a few cases have yet to be found in anything else. They seem most closely related to the legume-feeding Holarctic group that includes *C. hecla*, but this remains to be rigorously demonstrated. This is mainly a boreal group, with oreal relict populations south to the central Rocky Mountains. The southernmost Nearctic *Colias*, *C. philodice* and *C. eurytheme*, reach Guatemala but belong to a different group unlikely to be closely related to the Andean

species. Andean species apart, the only other Southern Hemisphere *Colias* is *C. electo*, with a scattered, relictual distribution in South Africa and montane tropical Africa and clearly of Palearctic provenance. Taken together, all of this suggests the classic scenario: penetration of the Andes by the *C. hecla* group in the Great American Interchange, followed by adaptive radiation and speciation. This fits the entire history of the Andean *Colias* into three million years.

Biochemical genetics ("molecular clocks") may give us a test of this scenario, if time points can be established to calibrate the rate of molecular evolution. In the meantime, it is not on its face unreasonable. The amount of morphological evolution in the Andean *Colias* is less than one routinely finds in exuberant insular lineages on similar time scales. Various plants whose occurence in the Andes has been attributed to the Great American Interchange have undergone substantial morphological change; there are woody Crucifers in northern Colombia and the world's largest lupine, *Lupinus paniculatus*, occurs in Peru, for example.

The biggest problem is *Colias ponteni*, also known as *C. imperialis*. It is the *Colias* allegedly from the Sandwich Islands (Hawaii) referred to in the quote from Dixey, above. It was put in its own genus, *Protocolias*, by Petersen (1963) on the basis of its remarkably primitive genitalia. Although it is indisputably the most primitive living (or recently extinct) *Colias*, no one really knows where it came from, and it has never been collected again. Shapiro (1993) tells its bizarre story. Gerardo Lamas (in litt.) believes the actual type locality was Cerro Tarn, near Port Famine, Magallanes (Chilean Patagonia). But this is in the heavily forested, perhumid part of the region, an unlikely *Colias* habitat. Another "Port Famine" butterfly, one actually collected by Darwin, was recently redis-covered in a different part of Magallanes in steppe, where it belongs (Herrera and Pérez d'A, 1989).

Biogeographers are perennially embarrassed by their inability to define criteria for identifying "centers of origin" (or to winnow the long list of contradictory criteria proposed by various authors). But by most such criteria, *Colias* should have originated in Laurasia, and the tip of South America is the last place to expect its center of origin. Thus *C. ponteni*, if truly Patagonian, must be rationalized away as a primitive species stranded in an out-of-the-way place and preserved (at least until the 1850s) by virtue of a lack of predators and competitors: a butterfly tuatara. But what of its relation (if any) to the other Andean *Colias*, and their Holarctic affinities?

To sum up: Descimon may be right, but declaring victory is decidedly premature. It would be very extraordinary if the entire Andean oreal fauna were of Holarctic origin. Just as even the far-north Andean oreal flora contains autochthonous elements (e.g., the Espeletiini, Compositae) as well as some derived from the lowlands — as noted by Descimon — so, too, the butterfly fauna is likely to be heterogeneous. The phenotypic convergences are so strong that biochemical-genetic and cladistic evi-

dence are absolutely necessary before any claim of homology can be accepted. As of now, there is no group, not even *Colias*, for which the claim of Holarctic origin can be considered fully established; and there is one — the hairstreaks — for which it has been virtually disproved.

The Pierids (Shapiro 1991a) and the blues, and perhaps *Colias*, all suggest ties to central Asia — presumably via a "Camelid scenario." Other groups that "should" partake of such a relationship are conspicuous by their absence in the Andes (*Lycaena*, *Parnassius*, various Holarctic Satyrids). Their absence alerts us to the possibility that the "ties" may not be real. Alternatively, the characteristic boreal-oreal fauna may not be as integrated a unit as we think.

The small Andean fritillaries (*Yramea*, Nymphalidae) have been linked with the small Holarctic ones (*Boloria*, *Clossiana*, *Brenthis*) and with the afro-tropical highland *Issoria*. Their true phylogenetic relationships are as yet unknown though two researchers (T. Pike and G. Lamas) are working on the problem. It now appears that the Austral *Yramea* feed on both Violaceae and Rosaceae (*Acaena*). This is precisely the pattern one finds in the boreal *Boloria*. The cynic will react to this news with a shrug and a "So what?"

## BACK TO THE IMPOVERISHMENT

Why are the Andean-oreal faunas so impoverished? The question is not why the Sierran oreal fauna is so big, but why the Andean one is so small. As we have seen, the emerging Sierran oreal biota was recruited from more or less nearby sources with a history of dealing with increasingly harsh climates. In fact, the South American oreal biota was either recruited from nearby lowland tropical sources, with little or no history of dealing with such climates, or from a distant Holarctic biota, better adapted but with limited access — or some combination of both. Either way, severe hardships existed which would tend to limit the number of lineages able to establish themselves successfully in just a few million years at most. And either way, we would expect a nearly insular situation — full of "vacant niches" and offering grand evolutionary opportunities. As Descimon (1986, p. 520) states:

> The impression — subjective, of course — that is felt by a naturalist looking at the rhopaloceran fauna of the Andes is one of "unsaturation": many ecological niches appear "empty," in particular many food plants remain without insects... Many times, wandering in the Great Andes, I stopped to look at a peculiar-looking biotope, in which I guessed there surely were special — and interesting, perhaps new! -butterflies. And there were none.

As noted above, the prominent role of Holarctic plants in the Andean oreal flora would facilitate the establishment of Holarctic butterflies already associated with them. Descimon and I agree that host utilization in the Andes is very spotty, and both of us predict evolutionary radiation

onto new hosts if in fact the oreal fauna is young and in disequilibrium. In this regard, recent data on host utilization are very striking.

Given the host relationships of the Polyommatini in the Holarctic, it is perhaps not very surprising that at least four species of Andean blues have now been found breeding on species of the large and diversified Holarctic genus *Astragalus* (Shapiro, unpublished). This Papilionaceous Legume would be on most lists of Great American Interchange arrivals in the region. It is very surprising, however, to find Pierini eating these plants.

The ancestral hosts of the Holarctic Pierini are mustard-oil-containing plants. These compounds (glucosinolates) are found in the Cruciferae, Capparidaceae, Resedaceae and Tropaeolaceae. The first three are phylogenetically close, while the fourth is generally considered much more distantly if at all related. Most of the Andean Pierini reared so far (various *Tatochila* and *Hypsochila*, *Reliquia*, *Phulia*, *Pierphulia*) feed on Crucifers and/or Tropaeolaceae. The Crucifers have been considered Great American Interchange arrivals in the Andes; they have undergone much evolution especially in the north, but unfortunately their fossil record is essentially nil. They are absent from the lowland tropics, except as introduced weeds. Capparidaceae occur as shrubs in the xeric habitats of South America. Their habitats being fairly young, they may be also. Tropaeolaceae is an autochthonous Neotropical family, including both high-Andean and Patagonian taxa. If the ancestors of *Tatochila* and *Hypsochila* came south from the Nearctic, they presumably had chemically preadapted resources waiting for them. It now appears, however, that the genus *Tatochila* (as presently construed, almost certainly polyphyletic) has shifted from these plants onto Papilionaceous Legumes twice and perhaps three times, and the sister-genus *Hypsochila* at least once. The Legume genera involved are *Astragalus*, *Vicia*, *Lathyrus*, and (probably in the past century or so) *Trifolium*. In one case (*Tatochila distincta*) the animal can be reared successfully on Crucifers, but apparently only uses Legumes in nature. (See Shapiro, 1986, 1990, 1991b.)

This is an exceedingly odd pattern, insofar as no other Crucifer-feeding pierine anywhere else in the world has made such a switch despite plenty of sympatry with appropriate Legumes. No "chemical bridge" between the plant taxa has been recognized (which is not to say one may not occur). What is strangest, though, is the repeated colonization of one plant group derivative from the Nearctic from another. The case for adaptive radiation in host selection in the oreal biome would be much stronger if the move had been onto plants of tropical American or Austral affinity!

## WHAT ABOUT PATAGONIA?

The Patagonian steppe is vegetationally and climatically reminiscent of the northern Great Basin desert of western North America, and for anyone who has worked in both areas, comparisons are inevitable.

The Patagonian butterfly fauna is exceedingly unbalanced, being dominated by the Pronophiline Satyrids. It is, however, fairly species-rich, and what is most striking is the fact that several of its lineages extend all the way to the northern Andes in the oreal biome. Yet, despite the climatic and vegetational diversity of this vast region, only a handful of species occur in the north, sometimes only one per lineage, while often several occur sympatrically in the south. Some of this may be merely an artifact of poor collecting in the Andes, and many of the Patagonian taxa, especially of Lycaenidae, are only very recently recognized. Moreover, the number of species is no reliable indicator of the "center of origin" for a genus, if such things can be inferred at all. Still, one gets the impression of groups that developed and radiated in the south and then moved north up the spine of the Andes, a pattern seemingly inconsistent with the bigger picture. It is not difficult to account for speciation in the south; the problem is to account for the lack of it in the north.

The high Andean-Patagonian connection is observed over a broad taxonomic spectrum. (See fig. 4.11 in Humphries and Parenti, 1986 and accompanying discussion; these authors give credence to a radical hypothesis — "Pacifica" — to account for it, but the timing would not work for butterflies. The postulated events are too early, requiring modern butterfly tribes to have differentiated in the Mesozoic.)

A peculiar problem affecting the blues, hairstreaks and pronophilini in Patagonia is very persistent convergence or stabilizing selection to the same color patterns — so that most of the hairstreaks found flying together look alike, even if not very closely related, and similarly for the Pronophilines. In both lineages there is a red blotch on the forewing underside, a theme found in some Holarctic Satyrids and in *Callipsyche behrii*, but never as a pervasive and defining trait of a whole fauna anywhere else!

The two major Satyrid lineages in South America are the Euptychiini, which are tropical and barely enter the temperate Argentine mid-latitudes, and the Pronophilini, which have speciated in two seeming bursts: one in the northern and central Andes associated with the Andean bamboos, the other in the *altiplano* and Patagonia on bunch-grasses. This second radiation is more diverse in lowland Argentina than in the Andean highlands (at both generic and specific levels). Some taxa, however, occur in both regions. The beautiful *Mariposa Plateada*, *Argyrophorus argenteus*, has a fascinating distribution which advertises Quaternary biotic movements. It occurs as relict local populations in the Chilean coast range and at high altitudes in the *cordillera* proper, in Coquimbo, San Juan, and Mendoza, thence south along the eastern foothills through the Uspallata Valley, to Aluminé, Zapala and Bariloche, reaching the immediate coast at Comodoro Rivadavia well south of its most austral inland outposts. Like the distribution of the Pierid *Tatochila theodice* (Shapiro, 1991b), this is in accord with the paleoclimatic reconstructions of Caviedes and Iriarte (1989) and Caviedes (1990). This work

envisions repeated north-south biotic migrations on both sides of the Andes, with movement sometimes from west to east and sometimes the reverse across the passes. Their model provides the best explanation of the Patagonian character of the Chilean Central Valley fauna. In the longer term, it implies the Patagonian butterfly fauna was already defined at the species level by the mid-Pleistocene, if not earlier. Unfortunately, these movements probably obliterated any biogeographic evidence bearing on the origins of that fauna -which may be approachable only molecularly or cladistically.

The Patagonian and Great Basin climates, and perhaps faunas, are probably of similar antiquity. Although the Patagonian fauna is much more unbalanced than the Great Basin one, insofar as it is dominated by Pronophilini, the overall species numbers are similar (Austin, 1985; Austin and Murphy, 1987). However fuzzy this statement, it certainly contrasts with the situation in the oreal zone. This once again forces us to think about why the Andean oreal fauna is so poor.

## CODA

In 1968, Dunbar discussed the eco-evolutionary status of polar biotas and concluded that their impoverishment was probably due — in a variety of ways — to their geologic recency; they were both ecologically and evolutionarily immature, and the processes of maturation in both series were likely to be mutually reinforcing. The basic problems faced by an emerging polar biota are the same as those confronting the oreal butterfly fauna, except that seasonal extremes are replaced by diel ones. In this regard it is non-trivial that boreal butterfly faunas are consistently much richer than Andean oreal ones, and entrain a much broader selection of lineages from the source faunas. This almost certainly reflects the role of the periglacial environment, whence major elements of both our Arctic and alpine-oreal Holarctic biota derive. The character of this environment has been much debated — tundra, steppe-tundra, steppe (French 1976, Lamb and Edwards 1988, Pielou 1991) and it is worth noting that the butterflies whose ranges suggest derivation from it also suggest a dry tundra or steppe-tundra, as shown in the work of Kostrowicki (1969). The possibility of an equivalent antecedent in the *altiplano* or in Patagonia for the Andean oreal butterflies remains effectively unexplored. If there was none, that in itself might explain much about that fauna.

Whether the Andean oreal butterflies originated from the Holarctic or from the adjacent lowlands, their low diversity is very likely a function of time. If it turns out that the high Andes are much older than we have thought, however, the mystery, already deep, will become unfathomable.

Descimon for having the courage to take on these issues and to gather what
scattered data there were bearing upon them. My own high-Andean work was
benefitted from three NSF grants, most recently BSR-83-0692. My Sierran
work has been underwritten mostly by California Agricultural Experiment
Station Project CA-D*-AZO-3994, "Climatic Range Limitation of Phytophagous
Lepidopterans." I thank Gerardo Lamas, Steve Courtney, Peggy Stern and José
Herrera G. for much stimulating discussion and insight, and Hansjürg Geiger,
Adam Porter, and Chris Nice for extraordinarily fruitful laboratory collabora-
tions. The profound ignorance displayed herein is, however, all mine.

I dedicate the paper to the memory of José Herrera G., who recognized the
problems very early, and of Adrienne Venables, who had she lived might have
solved them.

## LITERATURE CITED

ASHWORTH, A.C. & J.W. HOGANSON. 1993. The magnitude and rapidity of the
    climate change marking the end of the Pleistocene in the mid-latitudes of
    South America. Paleogeog., Paleoclimat., Paleoecol. 101: 263-270.

AUSTIN, G.T. 1985. Lowland riparian butterflies of the Great Basin and associated
    areas. J. Res. Lepid. 24: 117-131.

AUSTIN, G.T. & D.D. MURPHY. 1987. Zoogeography of Great Basin butterflies:
    patterns of distribution and differentiation. Great Basin Naturalist 47: 186-
    201.

BÁLINT, Z. 1993. A catalogue of polyommatine Lycaenidae (Lepidoptera) of the
    xeromontane oreal biome in the neotropics as represented in European
    collections. Reports Mus. Nat. Hist. Univ. Wis. (Stevens Point) 29: 1-42.

BÁLINT, Z. & K. JOHNSON. 1993a. New species of *Pseudolucia* Nabokov from Chile
    and Patagonia (Lepidoptera: Lycaenidae: Polyommatinae). Reports Mus.
    Nat. Hist. Univ. Wis. (Stevens Point) 27: 1-25.

——. 1993b. A new genus of Thecline-like Polyommatinae from the Andean
    region of South America (Lepidoptera: Lycaenidae: Polyommatinae). Ibid.
    28: 1-4.

BALLETTO, E. 1993. On some new genus-group and species-group names of
    Andean Polyommatini. Boll. Soc. Ent. Ital. (Genova) 124: 231-243.

BERGER, L.A. 1988. Systématique du genre *Colias* F. (Lepidoptera - Pieridae).
    Lambillionea 86:supplement, 68 pp.

BETANCOURT, J.L., T.R. VAN DEVENDER & P.S. MARTIN, eds. 1990. Pack Rat
    Middens. Univ. Arizona Press, Tucson. 467 pp.

BUFFON, G.L.L. 1962. Les Epoques de la Nature. Critical edition, J. Rogers, ed.
    Mem. Mus. Nat. D'Hist. Nat. (c), #10.

CAVIEDES, C.N. 1990. Rainfall variation, snowline depression and vegetational
    shifts in Chile during the Pleistocene. Climatic Change 16: 99-114.

CAVIEDES, C.N. & A. IRIARTE. 1989. Migration and distribution of rodents in
    central Chile since the Pleistocene: the paleogeographic evidence. J. Biogeog.
    16: 181-187.

CHABOT, B.F. & W.D. BILLINGS. 1972. Origins and ecology of the Sierran alpine
    flora and vegetation. Ecol. Monog. 42: 163-199.

CLAPPERTON, C.M. 1983. The glaciation of the Andes. Quat. Sci. Reviews 2: 83-
    155.

DESCIMON, H. 1986. Origins of Lepidopteran faunas in the high tropical Andes,
    pp. 500-532. In F. Vuilleumier and M. Monasterio (eds.), High Altitude
    Tropical Biogeography. Oxford, New York.

DIXEY, F.A. 1894. On the phylogeny of the Pierinae, as illustrated by their wing-markings and geographical distribution. Trans. Ent. Soc. London 42: 249-335.

DUNBAR, M.J. 1968. Ecological Development in Polar Regions: A Study in Evolution. Prentice Hall, Englewood Cliffs, N.J. 119 pp.

FRENCH, H.M. 1976. The Periglacial Environment. Longman, London. 309 pp.

FULLERTON, D.S. 1986. Chronology and correlation of glacial deposits in the Sierra Nevada, California. Quart. Sci. Reviews 5: 161-170.

GARTH, J. & J.W. TILDEN. 1963. Yosemite butterflies. J. Res. Lepid. 2: 1-96.

HERRERA, J. & V. PÉREZ D'A. 1989. Hallazgo en Chile de *Stuardosatyrus williamsianus* (Butler), 1868 y consideraciones sobre el género (Lepidoptera: Nymphalidae). Acta Ent. Chilena 15: 171-196.

HEUSSER, L.E. & J.E. KING. 1988. North America, pp. 193-236. In B. Huntley and T. Webb III (eds.), Vegetation History. Kluwer, Dordrecht.

HUMPHRIES, C.J. & L. PARENTI. 1986. Cladistic Biogeography. Clarendon Press, Oxford. 98 pp.

JOHNSON, K. 1992-93. Genera and species of the Neotropical "Elfin"-like hairstreak butterflies (Lepidoptera, Lycaenidae, Thecline). Reports Mus. Nat. Hist. Univ. Wis. (Stevens Point) 22: 1-279.

JOHNSON, K., L.D. MILLER & J. HERRERA G. 1992. *Eiseliana* and *Heoda*, high Andean and austral genera of the Neotropical Eumaeini (Lepidoptera: Lycaenidae). Acta Ent. Chilena 17: 107-146.

KLOTS, A.B. 1932. A generic revision of the Pieridae (Lepidoptera) together with a study of the male genitalia. Entomol. Americana 12(N.S.): 139-242.

KOSTROWICKI, A.S. 1969. Geography of the Palearctic Papilionoidea. Naukowe, Warsaw. 378 pp.

LAMB, H.F. & M.E. EDWARDS. 1988. The Arctic. pp. 519-555 in B. Huntley and T. Webb III (eds.), Vegetation History. Kluwer, Dordrecht.

MAJOR, J. & S.A. BAMBERG. 1967. Some cordilleran plants disjunct in the Sierra Nevada of California, and their bearing on Pleistocene ecological conditions, pp. 171-188. In H.E. Wright, Jr. and W.H. Osburn (eds.), Arctic and Alpine Environments. Indiana University Press, Bloomington.

MANI, M.S. 1968. Ecology and Biogeography of High-Altitude Insects. Junk, The Hague. 527 pp.

MERCER, J.H. & J.F. SUTTER. 1981. Late Miocene-earliest Pliocene glaciation in southern Argentina: implications for global ice-sheet history. Paleogeog., Paleoclimat., Paleoecol. 38: 185-206.

MOLNAR, P. & P. ENGLAND. 1990. Late Cenozoic uplift of mountain ranges and global climate change: chicken or egg? Nature 346: 29-34.

PETERSEN, B. 1963. The male genitalia of some *Colias* species. J. Res. Lepid. 1: 135-156.

PIELOU, E.C. 1991. After the Ice Age. Univ. Chicago Press. Chicago. 366 pp.

PORTER, A.H. & A.M. SHAPIRO. 1990. Genetics and biogeography of the *Oeneis chryxus* complex (Satyrinae) in California. J. Res. Lepid. 28: 263-276.

SCHRÖTER, C. & F. FIRBAS. 1934. Geographie der Pflanzen (Epiontologie). Handbuch der Naturwissenschaften, vol. 4. Jena.

SHAPIRO, A.M. 1978. The alpine butterfly fauna of Castle Peak, Nevada County, California. Great Basin Nat. 73: 443-482.

—— 1990. The life histories and behavior of the Patagonian-Fuegian white butterflies *Hypsochila microdice* and *H. galactodice* (Lepidoptera: Pieridae). J. New York Entomol. Soc., 98: 461-473.

——. 1991a. The zoogeography and systematics of the Argentine Andean and Patagonian pierid fauna. J. Res. Lepid., 28: 137-238.

——. 1991b. The biology and zoogeography of the Legume-feeding Patagonian-Fuegian white butterfly *Tatochila theodice* (Lepidoptera: Pieridae). J. New York entomol. Soc., 99: 251-260.

——. 1993. The proposed magellanic type-locality of *Colias imperialis* Butler (Lepidoptera: Pieridae). Acta Ent. Chilena 18: 77-82.

SHAPIRO, A.M., C.A. PALM & K.L. WCISLO. 1981. The ecology and biogeography of the butterflies of the Trinity Alps and Mount Eddy, northern California. J. Res. Lepid. 18: 69-152.

SIMPSON, G.G. 1980. Splendid Isolation. Yale University Press, New Haven. 266 pp.

STEHLI, F.G. & S.D. WEBB. 1985. The Great American Biotic Interchange. Plenum Press, New York.

WALLACE, A.R. 1876. The Geographical Distribution of Animals. 2 volumes. Harper, New York. 1056 pp.

WALTER, H. & E. MEDINA. 1969. La temperatura del suelo como factor determinante para la caracterización de los pisos subalpino y alpino en los Andes de Venezuela. Bol. Soc. Venez. Cienc. Nat. 115/116: 201-210.

WOLFE, J.A. 1985. Distribution of major vegetational types during the Tertiary, pp. 357-376. In E.T. Sundquist and W.S. Broecker (eds.), The Carbon Cycle and Atmospheric $CO_2$: Natural Variation, Archean to Present. American Geophysical Union, Washington, D.C.

# New Mexico butterflies: checklist, distribution and conservation

Steven J. Cary
4 Encantado Court, Santa Fe, New Mexico 87505

Richard Holland
1625 Roma NE, Albuquerque, New Mexico 87106

**Abstract.** This systematic list is intended to include every butterfly taxon observed in New Mexico. New Mexico has one of the most diverse butterfly faunas in the United States, with about 300 species. Taxon distribution in New Mexico is provided at the county level. Conservation status and concerns in New Mexico are also presented. The validity of questionable reports from this state are discussed and resolved where possible.

## ABOUT NEW MEXICO

New Mexico (NM) is the fifth largest state in the United States. Because of its location, NM supports elements of several regional butterfly faunas, including Great Plains, southern Rocky Mountains, Great Basin and Colorado Plateau, Sonoran and Chihuahuan Deserts, and Sierra Madre. Land surface elevations range from 914 m to 4012 m above sea level, supporting life zones from lower Sonoran to Arctic. Annual precipitation varies, primarily with latitude, from less than 25 cm to more than 110 cm. Number of frost free days varies locally from less than 80 to more than 220. The Continental Divide crosses the state from north to south and provides headwaters for major drainage basins such as the Colorado River, Rio Grande, Pecos River, and Arkansas River. Proximity to Mexico allows frequent summer influxes of subtropical species.

NM has always been a rural state with few resident lepidopterists. Reliable documentation of our butterfly fauna began in the 1870s and 1880s, but was sporadic until the 1960s. Many years of effort by the few NM lepidopterists were needed to gather enough information about our large, diverse state to issue this comprehensive state list. Now that all available information is compiled, it constitutes an impressive list, coming to about 300 species. Perhaps 95 percent of all breeding butterfly residents have been identified and confirmed. Much work remains to be done to identify remaining residents and to understand further the biology and distribution of known residents.

## FAUNAL LIST ORGANIZATION

Butterflies are presented here in the format and taxonomy of Scott (1986). Scott's approach does not adequately describe every situation in NM, however. In such cases the issues are discussed in NOTES, which follows the list. This document does not attempt to make taxonomic revisions or name new taxa.

Family names are given in upper case letters. For all taxa, genera, species and subspecies are italicized, with genera capitalized. Taxon authors are presented in normal font. A common name usually follows each scientific name.

Next are given the counties in which each taxon is known to occur. NM's 33 counties are shown in Figure 1 and abbreviated as follows:

| | | | | | |
|---|---|---|---|---|---|
| Bernalillo | Be | Harding | Ha | Roosevelt | Ro |
| Catron | Ca | Hidalgo | Hi | Sandoval | Sv |
| Chaves | Ch | Lea | Le | San Juan | SJ |
| Cibola | Ci | Lincoln | Li | San Miguel | SM |
| Colfax | Co | Los Alamos | LA | Santa Fe | SF |
| Curry | Cu | Luna | Lu | Sierra | Si |
| DeBaca | DB | McKinley | MK | Socorro | So |
| Dona Ana | DA | Mora | Mo | Taos | Ta |
| Eddy | Ed | Otero | Ot | Torrance | To |
| Grant | Gr | Quay | Qu | Union | Un |
| Guadalupe | Gu | Rio Arriba | RA | Valencia | Va |

The breeding or residency status of each taxon is given next. Residents overwinter and breed regularly in NM. Seasonal residents regularly fly in from subtropical areas during the warm season and may produce one or more generations before winter weather eliminates survivors. Strays wander into NM more or less by accident, with no known evidence of breeding. Hypothetical species are those whose presence here has been reported, then either refuted or seriously questioned, as signified by brackets []. Queries (?) indicate uncertainty. The final entry for some taxa is a numerical reference to one of the explanations in NOTES.

## SOURCES OF INFORMATION

This document represents the accumulated knowledge and personal observations of the authors, observations of associates, contents of personal collections, published papers, and other published accounts.

The following public collections were reviewed for NM specimens: Allyn Museum of Entomology (AME), American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Carnegie Museum (CM), Denver Museum of Natural History (DMNH), Eastern New Mexico University, Portales (ENMU), Illinois Natural History Survey (INHS), Los Angeles County Museum of Natural History (LACM), New Mexico Highlands University, Las Vegas (NMHU), New Mexico State University, Las Cruces (NMSU), United States Museum of Natural History, Smithsonian (USNM), University of Kansas (UK), and University of New Mexico, Albuquerque (UNM).

## HISTORICAL FOUNDATIONS AND ACKNOWLEDGMENTS

Many lepidopterists, professional and amateur, played key roles in the original observations assembled in this document. Key contributors to the knowledge of the NM butterfly fauna include:
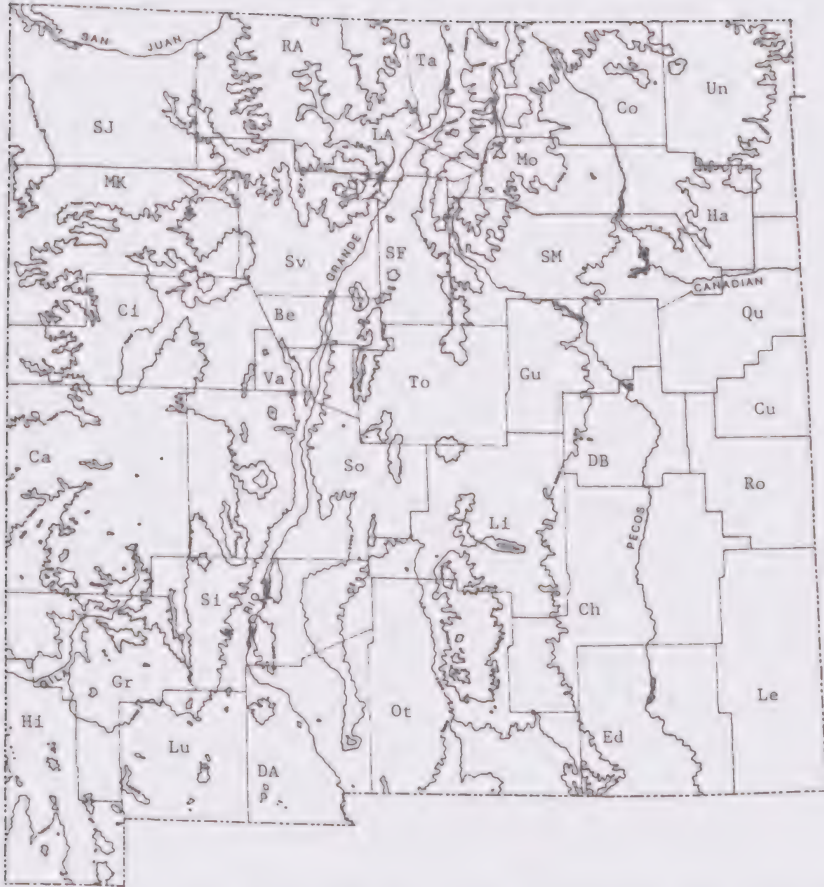
Fig. 1    Map of New Mexico indicating county abbreviations used in the text.
Contour lines for 2134 m (7000') and 2778 m (9000') elevations emphasize
prominent physiographic features. Major rivers are shown.

Frederick H. Snow and his students, from the University of Kansas,
contended with numerous frontier obstacles in the 1880s. They travelled
newly established railroad lines into NM and made collections near Las
Vegas, Santa Fe, Socorro, Deming and Silver City. Much of Snow's
collection remains at UK.

T. D. A. Cockerell was a faculty member of the NM College of Agricul-
tural and Mechanical Arts, a precursor of NMSU, in Las Cruces. He and
his associates performed entomological research and collected butter-
flies near Las Cruces, Las Vegas, Alamogordo and Ruidoso in the 1890s
and early 1900s. He published numerous scientific papers and described
several taxa. Some of his specimens remain in the collections at NMSU.

John Woodgate collected butterflies intensively in NM during the
period 1904 - 1925. He concentrated his work at Jemez Springs in the

Jemez Mountains, and near Fort Wingate in the Zuni Mountains. Several new taxa were described from material he collected.

John P. Hubbard directed the Endangered Species Program in the New Mexico Department of Game and Fish in the 1970s and 1980s. His biologists collected butterfly specimens in areas of special biological interest in NM, such as the Animas Mountains in the "bootheel" and Sierra Grande in Union County.

For many years Clifford D. Ferris, of the University of Wyoming, has researched butterflies in southwestern NM, emphasizing Grant County. From this work he has published several important scientific papers.

Michael E. Toliver studied NM butterflies statewide in the 1960s and 1970s and published scientific papers. He was the first to compile butterfly taxa into a NM fauna (Toliver and Holland, 1977). Toliver reviewed Snow's 100-year old specimens at UK, resolved several questions raised by Snow's reported observations, and updated his nomenclature. This document is dedicated to Mike, who first imagined it.

In addition to the pleasures of association with Drs. Ferris and Toliver, we have been encouraged and supported in our efforts by Drs. John M. Burns, Gregory S. Forbes, Paul A. Opler, Robert K. Robbins, James A. Scott, Ray E. Stanford, other members of the Lepidopterists' Society, and other observers of butterflies.

## CONSERVATION ISSUES

Despite NM's rural character, several NM butterflies warrant attention from a conservation perspective. Of principal interest are areas where there is endemism at the subspecies level, such as the Trans-Pecos desert mountains, the Sacramento Mountains, the Raton Mesa complex, and areas which support Pleistocene relicts.

The Trans-Pecos region of southern NM supports several taxa with limited distributions, such as *Fixsenia polingi*, *Chlosyne chinatiensis*, *Callophrys henrici solatus*, and *Agathymus mariae*. Populations of *F. polingi* are known only from three sites in NM: Organ Mountains, Guadalupe Mountains, and Capitan Mountains; plus a few places in west Texas (TX). Larvae feed only on oaks (*Quercus* spp.). It is not known how extensive or healthy these populations are as a whole, but the Guadalupe Mountains locality illuminates some of the issues. The Guadalupes straddle the NM/TX border. On the TX side, under the jurisdiction of Guadalupe Mountains National Park, larval host oaks thrive and *F. polingi* is widespread. On the NM side, however, where the Lincoln National Forest manages the land, host oaks and *F. polingi* are virtually nonexistent. Oaks and *F. polingi* are sensitive to land management practices such as grazing and fires in that area.

The Sacramento Mountains/Sierra Blanca range, just north of the Trans-Pecos is a prominent biogeographic island of disjunct montane butterflies. This range climbs to 3658 m elevation covers a large area, and is 150 km from comparable upland habitats to the north and west. Taxa

with relict Pleistocene populations there include: *Harkenclenus titus*, *Callophrys sheridanii*, *C. apama*, *Glaucopsyche lygdamus*, *Plebejus icarioides*, and *Phyciodes tharos* Type B. Although taxonomic study is still needed, most butterflies of interest here probably are differentiated at the subspecies level. Endemic subspecies already described for this area include *Speyeria atlantis capitanensis* and *Euphydryas anicia cloudcrofti*.

The Raton Mesa volcanic complex in northeast NM supports several taxa of interest due to its harsh climate, high elevation exceeding 2200 m, and long eastward extension from the Rocky Mountain Front Range into the Great Plains. Among the subspecific endemics in this area are *Oeneis alberta capulinensis*, *Speyeria atlantis ratonensis*, and *Poanes hobomok wetona*. Other species reported from here are unknown, or nearly so, from elsewhere in NM: *Polites peckius*, *Atrytonopsis hianna*, and *Satyrium liparops*. NM colonies of these species are very local and very few in number.

NM presently is a semi-arid state where water can be locally scarce. Wetland and riparian plants and animals prospered during the Pleistocene Ice Ages, when the southwestern US was much wetter than today. Drier post-Pleistocene climates restricted wetland and riparian butterflies to isolated pieces of their former ranges. Modern modification of hydrologic environments by human activities further fragments these habitats and may threaten survival of some obligate riparian butterflies, such as *Limenitis archippus*, *Speyeria nokomis* and *Ochlodes yuma*.

*L. archippus* larvae rely primarily on willows (*Salix* spp.) in a state where there has been large scale modification of natural hydrologic systems with resulting loss of native cottonwood/willow riparian forests. Dams built for management of floods and irrigation waters inundate much habitat. River flow downstream from such projects is reduced in volume as water is diverted to croplands. Floods are tamed, eliminating conditions necessary for germination of cottonwood seedlings and inviting invasion of salt cedar (*Tamarisk* sp.). The Desert Viceroy, *L. a. obsoleta,* was once studied for possible listing under the federal Endangered Species Act. It continues to survive in scattered populations in the Gila River, Rio Mimbres, Rio Grande and Pecos River valleys, but the size, number and health of these colonies remains unknown. Colonies along the Pecos seem to be the least numerous and the most isolated.

*Speyeria nokomis* is restricted to scarce montane wetland habitats which are vulnerable to adverse changes such as drainage for cultivation or excessive livestock grazing. Changes in the Sacramento Mountains, for another example, were related to logging in the early 20th century. After removal of trees, mountain valleys shed stormwater more quickly than under prior forested conditions. Through gullying and channel erosion, stream channels enlarged themselves to carry the increased runoff. Many miles of streamside wet meadows with lots of *nokomis* larval host *Viola nephrophylla* were cut by 5-m deep ephemeral arroyos and converted into dry meadows incapable of supporting *S. nokomis*.

   The other riparian species is *O. yuma*. We know of only one colony in NM; it is being described elsewhere as a new subspecies (Cary and Stanford, *in litt.*). Like *nokomis*, *yuma* relies on a single larval host, in this case *Phragmites australis* (Common Reed), which is an obligate riparian plant in NM. Hydrologic alterations near the colony site could lead to loss of the larval host, and then the butterfly. One potential threat to the colony is a proposed mining development nearby. A mill tailings impoundment could change the quality, quantity, flow regime or flow paths of seeps and springs which presently support the hostplant colony. Searches for other *O. yuma* colonies in NM have failed.

   Several NM species are recorded only from the state's bootheel-shaped southwest corner, in Hidalgo or adjacent counties. There, Sierra Madrean climates and plant communities support species which, although not rare in their core Mexican ranges, are unique in NM. The most important of these are residents for which only one or two NM colonies are known: *Pyrrhopyge araxes*, *Adopaeoides prittwitzi*, *Poanes melane*, *Atrytonopsis edwardsi*, *Agathymus polingi*, *Neophasia terlootii*, *Callophrys xami*, *Calephelis rawsoni*, and *Emesis ares*.

   Also important are Arctic/Alpine environments in north central NM. There, high peaks, marshes and ridges exceeding 3600 m elevation support Arctic Rocky Mountain species which are known from only one or two sites in NM: *Erebia magdalena*, *Boloria freija*, *Lycaena cuprea*, *Colias meadii*, and *Pieris occidentalis*. While not obviously threatened, the extremely limited occurrence of these species in NM is noteworthy.

## NEW MEXICO FAUNAL LIST

### HESPERIIDAE (SKIPPERS)

*Pyrrhopyge araxes* (Hewitson). Araxes Skipper. Hi. Resident.

[*Proteides mercurius* (Fabricius)]. Hypothetical. Note 1.

*Epargyreus clarus* (Cramer). Silver-Spotted Skipper. Be,Ca,Co,DA,Gr,Hi,Li, LA,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

[*E. exadeus* (Cramer)]. Hypothetical. Note 1.

*Polygonus leo* (Gmelin). Violet Skipper. Ed,Hi,Ot,Si,To. Stray.

*Chioides catillus* (Cramer). Silver-Banded Skipper. Hi,Lu. Stray.

*Zestusa dorus* (W. H. Edwards). Short-Tailed Arizona Skipper. Be,Ca,Co,Gr, Hi,Li,MK?,Mo,Ot,RA,Sv,SM,SF,Si,So,Ta,To,Va. Resident.

*Codatractus arizonensis* (Skinner). Arizona Skipper. Hi,Lu. Stray.

*Urbanus proteus* (Linnaeus). Blue-Green Long-Tailed Skipper. Hi. Stray.

*U. dorantes* (Stoll). Lilac-Banded Longtail. Hi. Stray.

[*U. simplicius* (Stoll)]. Hypothetical. Note 2.

*U. procne* (Plotz). Brown Longtail. Hi. Stray.

[*Astraptes fulgerator* (Walch)]. Hypothetical. Note 3.

*Autochton cellus* (Boisduval and Leconte). Gold-Banded Skipper. Ca,Gr,Hi. Resident.

*Achalarus casica* (Herrich-Schaffer). Desert Hoary Edge. Gr,Hi,Lu. Resident.

[*Thorybes bathyllus* (J. E. Smith)]. Hypothetical. Note 4.

*T. pylades* (Scudder). Northern Cloudywing. Be,Ca,Ch,Ci,Co,DA,Ed,Gr,Ha,Hi,
    LA,Lu,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,To,Un. Resident.

*T. mexicanus* (Herrich-Schaffer). Mountain Cloudywing. Be,Ca?,Co,Gr,Li,LA,
    Mo,Ot,RA,Sv,SJ,SM,SF,Ta. Resident.

*T. drusius* (W. H. Edwards). White-Edged Cloudywing. Hi. Resident.

*Cogia hippalus* (W. H. Edwards). White-Edged Skipper. DA,Hi,Lu. Resident.

*C. caicus* (Herrich-Schaffer). Arizona White-Edged Skipper. Ca,Gr, Hi,Lu,Si.
    Resident.

*Staphylus ceos* (W. H. Edwards). Redhead Sootywing. Be,Ca,DA,Ed,Gr,Hi,Lu,
    Ot,Si. Resident.

[*Xenophanes trixus* (Stoll)]. Hypothetical. Note 49.

*Systasea pulverulenta* (R. Felder). Texas Powdered Skipper. Ed. Resident.

*S. zampa* (W. H. Edwards). Arizona Powdered Skipper. Ca,DA,Ed,Gr,Hi,Lu,
    Ot,Si. Resident.

[*Grais stigmaticus* (Mabille)]. Hypothetical. Note 49.

*Timochares ruptifasciatus* (Plotz). Brown-Banded Skipper. Gr. Stray.

*Chiomara asychis* (Stoll). White Patch Skipper. Hi. Stray.

*Erynnis icelus* (Scudder and Burgess). Aspen Duskywing. Be,Ca,Ci,Co,Gr,Li,
    LA,Mo,Ot,RA,Sv,SJ,SM,SF,Si,Ta,To,Un. Resident.

*E. brizo* (Boisduval and Leconte). Banded Oak Duskywing. All counties.
    Resident.

*E. juvenalis clitus* (W. H. Edwards). Sonoran Oak Duskywing. Hi. Resident.
    Note 5.

[*E. j. juvenalis* (Fabricius)]. Hypothetical. Note 6.

*E. telemachus* Burns. Gambel Oak Duskywing. All counties except Cu,DB,Gu,
    Hi,Le,Qu,Ro. Resident.

[*E. propertius* (Scudder and Burgess)]. Hypothetical. Note 7.

*E. meridianus* Bell. Southwestern Oak Duskywing. Be,Ca,Ch,DA,Ed,Gr,Ha?,
    Hi,Li,Lu,Ot,Sv,Si,So,To. Resident. Note 8.

*E. scudderi* (Skinner). Scudder's Duskywing. Hi. Resident?

*E. horatius* (Scudder and Burgess). Brown Duskywing. Co,Ed?,Ha,Li,Mo,Ot,
    Qu,RA,Sv,SM,SF,Un. Resident. Note 9.

*E. tristis tatius* (W. H. Edwards). White-Edged Duskywing. Ca,Ch,DA,Ed,Gr,
    Gu,Hi,Li,Lu,Ot,Si,So. Resident.

[*E. martialis* (Scudder)]. Hypothetical. Note 10.

*E. pacuvius* (Lintner). Buckthorn Duskywing. Be,Ca,Ci,Co,Gr,Hi,Li,LA,MK,
    Mo,RA,Sv,SJ,SM,SF,Si,So,Ta,To. Resident.

*E. funeralis* (Scudder and Burgess). Streamlined Duskywing. All counties
    except Co,Cu,DB,Qu,RA,Ro,Va. Resident.

*E. afranius* (Lintner). Bald Duskywing. All counties except Ch,Ci?,Co,DA,DB,
    Ed?,Le,Lu,Ot?,Ro,Va. Resident. Note 11.

*E. persius* (Scudder). Hairy Duskywing. Be,Ca,Ci?,Co,Gr,LA,Mo?,Ot,RA,Sv, SJ,SF,Si?,Ta,To,Un. Resident. Note 11.

*Pyrgus centaureae loki* Evans. Alpine Checkered Skipper. Co,Mo,RA,SM,SF, Ta. Resident.

*P. xanthus* W. H. Edwards. Mountain Checkered Skipper. Ca,Ci,Co,Li,LA, MK,Mo,Ot,RA,Sv,SM,So. Resident.

*P. scriptura* (Boisduval). Small Checkered Skipper. Be,Ca,Ch,Ci,DA,Ed,Ha, Hi, Lu,MK,Ot,Sv,SM,SJ,Si,So,To,Un. Resident.

*P. communis communis* (Grote). Checkered Skipper. All counties. Resident. Note 12.

*P. c. albescens* (Plotz). White Checkered Skipper. Ca,Ci,Gr,Gu,Hi,Li,MK,Qu, So. Resident. Note 12.

*P. oileus* (Linnaeus). Tropical Checkered Skipper. Hi. Seasonal Resident.

*P. philetas* W. H. Edwards. Desert Checkered Skipper. Hi,Lu. Resident.

*Heliopetes domicella* (Erichson). Banded White Skipper. Lu. Stray.

*H. ericetorum* (Boisduval). Great Basin White Skipper. Ca, MK,RA,SJ. Resident.

*Celotes nessus* (W. H. Edwards). Streaky Skipper. Ca,Ch,DB,DA,Ed,Gr,Gu, Ha,Hi,Li,Lu,Ot,Qu,SM,Si,So,Un. Resident.

*Pholisora catullus* (Fabricius). Common Sootywing. All counties except LA, Mo,RA,SJ,Va. Resident.

*P. mejicana* (Reakirt). Mexican Sootywing. Be,Co,Ed?,Li,Mo?,Ot,SM,SF,To, Un. Resident.

*Hesperopsis libya* (Scudder). Great Basin Sootywing. SJ. Resident.

*H. alpheus* W. H. Edwards. Saltbush Sootywing. Be,Ch,Ci,Co,DB,DA,Ed,Gr, Hi,MK,Ot,RA,Sv,SJ,Si,So. Resident. Note 13.

*Piruna pirus* (W. H. Edwards). Russet Skipperling. Be,Ca?,Co,Gr?,LA,Mo,RA, Sv,SJ,SM,SF,Si?,So,Ta,To,Un. Resident.

*P. polingii* (Barnes). Spotted Skipperling. Ca,Gr,Li,Ot,Si. Resident.

*Lerema accius* (J. E. Smith). Clouded Skipper. Ed,Hi. Stray.

*Ancyloxypha numitor* (Fabricius). Least Skipperling. Un. Resident.

*A. arene* (W. H. Edwards). Tropical Least Skipperling. Ca,Ch,DA,Ed,Gr,Gu, Hi,Ot,Si,So. Resident.

*Oarisma garita* (Reakirt). Western Skipperling. Be,Ca,Ci,Co,Gr,Li,LA,MK, Mo,Ot,RA,Sv,SM,SF,So,Ta,To,Un. Resident.

*O. edwardsii* (Barnes). Edwards' Skipperling. Be,Ch,Ci,Co,DA,Ed,Gr,Ha,Hi, Li,LA,MK,Mo,Ot,RA,Sv,SM,SF,Si,So,Ta,To,Un. Resident.

*Copaeodes aurantiacus* (Hewitson). Orange Skipperling. Be,Ca,Ch,Cu,DB,DA, Ed,Gr,Gu,Hi,Li,Lu,Ot,Qu,Ro,SM,Si,So,Va. Resident.

*Adopaeoides prittwitzi* (Plotz). Black-Veined Skipperling. Hi. Resident.

*Hylephila phyleus* (Drury). Fiery Skipper. Be,Ca,Ch,Cu,DB,DA,Ed,Gr,Hi,Le, Lu?, Ot,Ro,Si,So. Resident.

*Yvretta rhesus* (W. H. Edwards). Prairie Cobweb Skipper. Ca,Ci,Co,Ed?,Gr,Li, MK,Mo,Ot,Qu,RA,Sv,SM,SF,Ta,Un. Resident.

*Y. carus* (W. H. Edwards). Mexican Cobweb Skipper. Be,DA,Ed,Gr,Hi,Qu,Un. Resident.

*Stinga morrisoni* (W. H. Edwards). Morrison's Silver Spike. Ca,Ch,Ci,Co,Ed, Gr,Li,LA,Lu,MK,Mo,Ot,RA,Sv,SJ,SM,Si,So,Ta,To. Resident.

*Hesperia uncas uncas* W. H. Edwards. White-Vein Skipper. All counties except DA,Hi,Lu,Si. Resident.

*H. uncas lasus* (W. H. Edwards). Arizona White-Vein Skipper. Gr. Resident.

*H. juba* (Scudder). Jagged-Border Skipper. RA,Sv,SJ. Resident.

*H. comma colorado* (Scudder). Colorado Branded Skipper. Co,LA,Mo,RA,Sv, SM,Ta,Un. Resident.

*H. c. susanae* L. Miller. Susan's Branded Skipper. Ca,Ci,Gr,Li,MK, SJ. Resident.

*H. woodgatei* (R. C. Williams). Autumn Skipper. Ca,Ci,Ed,Gr,LA,MK,Sv,SM, SF,Si,So. Resident. Note 14.

*H. pahaska* (Leussler). Yellow-Dust Skipper. All counties except DB,Gu,Le. Resident.

*H. viridis* (W. H. Edwards). Black-Dust Skipper. All counties except DA,Le, LA,Lu. Resident. Note 15.

*H. nevada* (Scudder). Montane Skipper. Co,LA,Mo,RA,Sv,SM,SF,Ta. Resident.

[*Polites peckius* (W. Kirby)]. Hypothetical. Note 49.

*P. sabuleti* (Boisduval). Saltgrass Skipper. RA,Sv,SJ,SF,Ta. Resident.

*P. draco* (W. H. Edwards). Rocky Mountain Skipper. Ci,Co,LA,MK,Mo,RA,Sv, SM,SF,So,Ta. Resident.

*P. themistocles* (Latreille). Tawny-Edged Skipper. Ca,Ci,Co,LA,Li,MK,Mo, Ot,RA,Sv,SM,SF,Ta,Un. Resident.

*P. origenes rhena* (W. H. Edwards). Western Cross-Line Skipper. Co,SM?,Un. Resident.

[*P. mystic* (W. H. Edwards)]. Hypothetical. Notes 16,18.

[*P. vibex* (Geyer)]. Hypothetical. Note 17.

[*Pompeius verna* (W. H. Edwards)]. Hypothetical. Note 18.

*Atalopedes campestris* (Boisduval). Sachem. All counties except Ca,Ci,LA,MK, RA,Ta,To,Va. Resident.

*Atrytone logan* (W. H. Edwards). Delaware Skipper. Ch,Cu,DB,Ed,Gu,Ha,Li, Mo,Qu,Ro,SM,Un. Resident.

*Ochlodes sylvanoides* (Boisduval). Western Skipper. RA,Sv,SM?. Resident.

*O. yuma* (W. H. Edwards). Giant Reed Skipper. Ta. Resident.

*Paratrytone snowi* (W. H. Edwards). Snow's Skipper. Ca,Ci,Co,Gr,LA,MK,Mo, Sv,SM,SF,Si,So,Ta. Resident.

*Poanes hobomok wetona* Scott. Wetona Skipper. Co. Resident.

[*P. zabulon* (Boisduval and Leconte)]. Hypothetical. Note 19.

*P. taxiles* (W. H. Edwards). Golden Skipper. Be,Ca,Ci,Co,DA,Gr,Li,LA,MK, Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*P. melane vitellina* (Herrich-Schaffer). Melane Skipper. Hi. Resident.

[*Euphyes bimacula* (Grote and Robinson)]. Hypothetical. Note 20.

*E. vestris* (Boisduval). Dun Skipper. Be,Ca,Co,Ed,Gr,Ha,Li,LA,Mo,Ot,RA,Sv, SJ,SM,SF,So,Ta,To,Un. Resident.

*Atrytonopsis hianna* (Scudder). Dusted Skipper. Co,LA. Resident.

*A. deva* (W. H. Edwards). Desert Dusted Skipper. Ca,Gr,Hi,Si. Resident.

[*A. elissa* (Godman)]. Hypothetical. Note 49.

*A. lunus* (W. H. Edwards). Violet Dusted Skipper. DA,Gr,Hi. Resident.

*A. vierecki* (Skinner). Viereck's Dusted Skipper. All counties except DB,Le,LA, Ro,Ta,Va. Resident. Note 21.

*A. pittacus* (W. H. Edwards). White-Bar Dusted Skipper. Ca,Gr,Hi, Lu. Resident.

*A. python* (W. H. Edwards). Yellow-Spot Dusted Skipper. Be,Ca,Ch,Ci,DA,Ed, Gr,Gu?,Hi,Li,LA,Lu,MK,Ot,RA,Sv,SF?,Si,So,To. Resident. Note 22.

*A. edwardsi* Barnes and McDunnough. Rounded Dusted Skipper. Hi. Resident.

*Amblyscirtes simius* W. H. Edwards. Hilltop Little Skipper. Be,Ch,Ci?,Co,Cu, DA,Ed,Gr,Gu,Ha,Hi,Li,LA,Mo,Ot,RA,Sv,SF,Un,Va? Resident.

*A. exoteria* (Herrich-Schaffer). Sonoran Little Skipper. Ca,Gr,Hi, Si. Resident.

*A. cassus* W. H. Edwards. Tawny Little Skipper. Ca,Ci,Co,Gr,Hi,Li,LA,MK,Ot, RA,Sv,SM,Si,So. Resident.

*A. aenus* W. H. Edwards. Bronze Little Skipper. All counties except Le,LA,Ro, SJ,Va. Resident.

*A. oslari* (Skinner). Prairie Little Skipper. Be,Ca,Ch,Ci?,Co,DA,Ed,Gr,Ha,Hi, Li,LA,MK,Mo,Ot,Qu,RA,Sv,SM,SF,Ta,To,Un,Va? Resident. Note 23.

*A. texanae* Bell. Southwest Little Skipper. Ca,Ch,Ci,DA,Ed,Gr,Hi,Lu,Ot,Qu, Si. Resident.

*A. nereus* (W. H. Edwards). Creamy Little Skipper. Ca,Ed,Gr,Hi,Si. Resident.

*A. nysa* W. H. Edwards. Mottled Little Skipper. DB,DA,Ed,Hi,Le,Ot?,Qu,Ro. Resident.

*A. eos* (W. H. Edwards). Dotted Little Skipper. All counties except Ca,Ci,LA, MK,RA,SJ,SF,Ta. Resident. Note 24.

*A. vialis* (W. H. Edwards). Black Little Skipper. Co,LA,RA,Sv,Ta,Un. Resident.

*A. phylace* (W. H. Edwards). Redhead Little Skipper. Be,Ci,Co,Gr,Li,LA,MK, Mo,Ot,RA,Sv,SM,So,To,Un. Resident.

[*A. fimbriata* (Plotz)]. Hypothetical. Note 25.

*Lerodea eufala* (W. H. Edwards). Gray Skipper. DA,Ed,Gr,Hi, Le,Lu,Ro. Stray.

*Calpodes ethlius* (Stoll). Canna Skipper. Ro. Stray.

## MEGATHYMIDAE (GIANT SKIPPERS)

*Agathymus neumoegeni* (W. H. Edwards). Tawny Giant Skipper. Ca,Ch,DA, Ed,Gr,Lu,Ot. Resident. Note 26.

*A. aryxna* (Dyar). Arizona Giant Skipper. Gr,Hi,Lu. Resident.

*A. mariae* (Barnes and Benjamin). Lechuguilla Giant Skipper. Ch, Da,Ed,Ot. Resident.

*A. polingi* (Skinner). Little Giant Skipper. Hi. Resident.

*Megathymus yuccae* (Boisduval and Leconte). Yucca Giant Skipper. Be,Ca,Ch, Ci,DA,Ed,Gr,Hi,Li,LA,Lu,Mo,Ot,RA,Ro,Sv,SF,So,Ta,To,Un,Va. Resident. Note 27.

*M. streckeri streckeri* (Skinner). Plains Yucca Skipper. Be,Ci?,Li,MK,Ot,RA, Sv,SJ,SF,To? Resident.

*M. s. texanus* Barnes and McDunnough. Texas Yucca Skipper. Co,Cu,DB,Gu, Ha,Le?,Qu,Ro,SM,Un. Resident.

*M. ursus* Poling. Desert Yucca Skipper. DA,Ed,Hi,Ot,To. Resident. Note 28.

## PAPILIONIDAE (SWALLOWTAILS)

*Parnassius phoebus pseudorotgeri* Eisner. Small Apollo. Co,Mo,RA, SM,SF,Ta. Resident.

*Battus philenor* (Linnaeus). Pipevine Swallowtail. Be,Ca,Ch,Ci,Co,DB,DA,Ed, Gr,Ha,Hi,Le,Li,Lu,MK,Mo,Ot,Qu,Ro,Si,So,Ta,To,Un. Resident.

*B. polydamas* (Linnaeus). Gold Rim. Lu. Stray.

*Papilio polyxenes asterius* Stoll. Eastern Black Swallowtail. All counties except Va? Resident. Note 29.

*P. bairdii* W. H. Edwards. Western Black Swallowtail. Be,Ca,Ci,Gr?,LA,MK, Ra,Sv,SJ,SF,So?,Ta,To? Resident. Note 30.

*P. zelicaon* Lucas. Anise Swallowtail. Be,Ci,Co,LA,MK,Mo,RA,Sv,SJ, Ta,To. Resident.

*P. indra minori* Cross. Cliff Swallowtail. MK,Sv?,SJ? Resident.

*P. cresphontes* Cramer. Giant Swallowtail. Ch,DB,Ed,Gr,Hi,Lu,Ot, Ro,So,To. Seasonal Resident. Note 31.

*P. ornythion* Boisduval. Ornythion Swallowtail. Ch,Da,Ed. Stray.

*P. rutulus* Lucas. Western Tiger Swallowtail. Be,Ca,Ci,Co,Gr,Hi,Li,LA,MK, Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*P. multicaudatus* W. F. Kirby. Two-Tailed Tiger Swallowtail. All counties except Cu,Le. Resident.

*P. eurymedon* Lucas. Pale Tiger Swallowtail. LA,MK?,Mo,RA,Sv,SM. Resident. Note 32.

[*P. pilumnus* Boisduval]. Hypothetical. Note 33.

[*P. troilus* Linnaeus]. Hypothetical. Note 34.

*P. palamedes* Drury. Palamedes Swallowtail. Co. Stray.

## PIERIDAE (WHITES AND SULPHURS)

*Neophasia menapia* (C. and R. Felder). Pine White. Be,Ca,Ci,Co,Gr,Li,LA, MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To. Resident.

*N. terlootii* (emended) Behr. Mexican Pine White. Hi. Resident.

*Appias drusilla* (Cramer). Tropical White. Gr. Stray.

*Pieris beckerii* W. H. Edwards. Great Basin White. Co,MK?,RA,SJ. Resident.

*P. sisymbrii* Boisduval. Spring White. All counties except Ch,Cu,DB,Gu,Le, LA,Qu?,Ro. Resident. Note 35.

*P. protodice* Boisduval and Leconte. Checkered White. All counties. Resident.

*P. occidentalis* Reakirt. Peak White. Ta. Resident. Note 36.

*P. napi mcdunnoughi* Remington. Veined White. Be,Co,LA,MK,Mo,RA,Sv,SM, SF,Ta. Resident.

*P. n. mogollon* Burdick. Mogollon Veined White. Ca,Li,Ot. Resident. Note 37.

*P. rapae* (Linnaeus). European Cabbage White. All counties except MK? Resident.

*Ascia monuste* (Linnaeus). Great Southern White. DA. Stray.

*A. josephina* (Godart). Giant White. Be. Stray.

*Euchloe ausonides* (Lucas). Creamy Marblewing. Be,Co,Mo,RA,SM,SF, Ta,Un. Resident.

*E. hyantis lotta* Beutenmuller. Western Marble. DA,Gr,Hi,Lu,MK,RA,Sv,SJ, Si,So,Ta. Resident.

*E. olympia* (W. H. Edwards). Olympia Marblewing. Cu,Gu,Ha,Qu,Un. Resident.

*Anthocharis cethura pima* W. H. Edwards. Pima Orangetip. DA,Gr,Hi, Lu. Resident.

*A. sara* Lucas. Sara Orangetip. All counties except Ch,Co,DB,Ed, Le,Ro,Un. Resident. Note 38.

*Colias philodice* Godart. Common Sulphur. All counties. Resident.

*C. eurytheme* Boisduval. Orange Sulphur. All counties. Resident.

*C. alexandra alexandra* W. H. Edwards. Queen Alexandra's Sulphur. Ca,Co, Gr,LA,MK?,Mo,RA,Sv,SM,SF,Si,Ta,To. Resident.

*C. meadii meadii* W. H. Edwards. Mead's Sulphur. Co,Ta. Resident.

*C. scudderii ruckesi* Klots. Scudder's Willow Sulphur. Co,Mo,SM, SF,Ta. Resident. Note 39.

*Zerene cesonia* (Stoll). Dogface. All counties except LA. Resident.

*Anteos clorinde* (Godart). Ghost Brimstone. Co,Hi,SM. Stray.

*A. maerula* (Fabricius). Yellow Brimstone. Hi. Stray.

*Phoebis sennae* (Linnaeus). Cloudless Giant Sulphur. All counties except Ci, Ha,LA,Mo,RA,Sv,SJ. Resident.

*P. philea* (Johansson). Orange-Barred Giant Sulphur. Gr,Hi,Ot. Stray.

*P. agarithe* (Boisduval). Orange Giant Sulphur. Ca,Ed,Gr,Ha,Hi,Le. Stray.

*Kricogonia lyside* (Godart). Guayacan Sulphur. Ed,Gr,Hi,Le,Li,Lu, Qu,Ro,Un. Seasonal Resident.

*Eurema daira* (Godart). Barred Sulphur. Hi. Stray.

*E. boisduvalianum* (C. and R. Felder). Boisduval's Yellow. Ed,Hi, Lu. Seasonal Resident.

*E. mexicanum* (Boisduval). Mexican Yellow. All counties except Cu,DB,Gu,Ha, LA,Qu,RA. Resident.

[*E. salome* (C. and R. Felder)]. Hypothetical. Note 40.

*E. proterpia* (Fabricius). Tailed Orange. DA,Gr,Hi,Ot. Seasonal Resident.

*E. lisa* (Boisduval and Leconte). Little Sulphur. Cu,Ed,Hi,Le,Li, Qu,Ro,SJ,Sv. Resident.

*E. nise* (Cramer). Blacktip Sulphur. Hi. Seasonal Resident.

*E. nicippe* (Cramer). Sleepy Orange. All counties. Resident.

*Nathalis iole* Boisduval. Dwarf Yellow. All counties. Resident.

[*Enantia melite* (Johansson)]. Hypothetical. Note 2.


## LYCAENIDAE (LITTLE BUTTERFLIES)

*Lycaena arota virginiensis* (W. H. Edwards). Tailed Copper. Be,Ca,Ci,Co,LA, MK,Mo,RA,Sv,SM,SF,Ta,To,Un. Resident.

*L. xanthoides dione* (Scudder). Plains Gray Copper. Un. Resident.

*L. cuprea snowi* (W. H. Edwards). Lustrous Copper. Ta. Resident.

*L. rubida* (Behr). Ruddy Copper. Ra,Ta. Resident.

*L. heteronea heteronea* (Boisduval). Blue Copper. Co,RA,Sv,Ta. Resident.

*L. helloides* (Boisduval). Purplish Copper. Co,LA,Mo,RA,Sv,SJ,SM, SF,Ta. Resident.

[*L. nivalis* (Boisduval)]. Hypothetical. Note 41.

*Hypaurotis crysalus crysalus* (W. H. Edwards). Colorado Hairstreak. Be,Ca, Ci,Co,Gr,Li,LA,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

[*Eumaeus minijas* (Hubner)]. Hypothetical. Note 2.

*Atlides halesus* (Cramer). Great Blue Hairstreak. Be,Ca,Ch,Ci,DA,Ed,Gr,Gu, Hi,Li,LA,Lu,MK,Ot,RA,Sv,SJ,SM?,SF,Si,So,Ta,To,Va. Resident.

*Phaeostrymon alcestis alcestis* (W. H. Edwards). Soapberry Hairstreak. Ch, DB,Ed,Gu,Ha,Li,Qu,Ro,SM,Un. Resident.

*P. a. oslari* (Dyar). Southwestern Soapberry Hairstreak. Gr,Hi. Resident.

*Harkenclenus titus titus* (Fabricius). Coral Hairstreak. Li. Resident. Note 42.

*H. t. immaculosus* (W. P. Comstock). Great Basin Coral Hairstreak. Be,Co,RA, Sv,SM,SF,Ta,To,Un. Resident.

*Satyrium behrii crossi* (Field). Behr's Hairstreak. Be,Co,MK,RA,Sv,SJ,SM,SF, To,Un. Resident.

*S. sylvinum sylvinum* (Boisduval). Western Willow Hairstreak. Ca,MK,RA,Sv, SJ,SM?,Ta. Resident.

*S. calanus godarti* (Field). Banded Hairstreak. Be,Co,LA,Mo,RA,Sv,SM,SF, Ta,Un. Resident.

*S. liparops strigosum* (Harris). Striped Hairstreak. Un. Resident.

*S. saepium* (Boisduval). Buckthorn Hairstreak. LA. Resident.

*Ministrymon leda* (W. H. Edwards). Mesquite Hairstreak. Ca,Ch,Ci,DA,Ed, Gr,Hi,Li,MK,Ot,RA,SJ,SF,To. Resident.

*Callophrys apama apama* (W. H. Edwards). Green Hairstreak. Ca,Ci,Gr,Li, MK,Ot,SJ. Resident.

*C. a. homoperplexa* Barnes and Benjamin. Rocky Mountain Green Hairstreak. Co,LA,RA,Sv,SM,SF,Ta,Un. Resident.

*C. sheridanii sheridanii* (W. H. Edwards). White-Line Green Hairstreak. Li,Ot,RA. Resident. Note 42.

*Callophrys spinetorum* (Hewitson). Blue Mistletoe Hairstreak. Be,Ca,Ci,Co, DA,Ed,Gr,Li,LA,Lu,MK,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To. Resident. Note 43.

*C. grynea siva* (W. H. Edwards). Juniper Hairstreak. All counties except Le. Note 44.

*Callophrys xami* (Reakirt). Succulent Hairstreak. Gr. Resident.

*C. mcfarlandi* (P. Ehrlich and Clench). Beargrass Hairstreak. Be,Ch,Ci,Co, Cu,DB,DA,Ed,Gu,Ha,Li,Lu,Mo,Ot,Qu,Ro,Sv,SM,So,To,Un. Resident. Note 45.

*C. augustus iroides* (Boisduval). Brown Elfin. Ca,Gr,Hi,Lu,RA,Sv,SJ. Resident. Note 46.

*C. fotis* (Strecker). Desert Elfin. Ci,MK,Sv,SJ. Resident.

*C. polios* Cook and Watson. Hoary Elfin. Co,MK,RA,Sv,SM. Resident.

*C. henrici solatus* Cook and Watson. Trans-Pecos Elfin. Da,Ed. Resident.

*C. eryphon* (Boisduval). Western Pine Elfin. Ca,Ci,Co,Gr,LA,MK,Mo,Ot?,RA, Sv,SJ,SM,SF,So?,Ta. Resident.

*Fixsenia favonius autolycus* (W. H. Edwards). Oak Hairstreak. Co,Cu,Ha,Li, Mo,Ot,Qu,SM,Un. Resident. Note 47.

*F. f. ilavia* (Beutenmuller). Southwestern Oak Hairstreak. Gr. Resident.

*F. polingi* (Barnes and Benjamin). Poling's Hairstreak. DA,Ed,Li. Resident. Note 48.

*Strymon melinus* Hubner. Gray Hairstreak. All counties. Resident.

[*S. bebrycia* (Hewitson)]. Hypothetical. Note 49.

*S. columella* (Fabricius). Columella Hairstreak. Hi. Stray.

*Erora quaderna* (Hewitson). Arizona Hairstreak. Ca,Gr,Hi,Lu,Si,So, To. Resident.

*Brephidium exile* (Boisduval). Western Pygmy Blue. All counties. Resident.

*Leptotes cassius* (Cramer). Tropical Striped Blue. RA. Stray.

*L. marina* (Reakirt). Striped Blue. All counties. Resident.

*Zizula cyna* (W. H. Edwards). Tiny Blue. Ed,Lu. Seasonal Resident.

*Hemiargus ceraunus gyas* (W. H. Edwards). Southern Blue. Ca,DA,Ed,Gr,Hi, Lu,Ot,Si,So. Resident.

*H. isola* (Reakirt). Solitary Blue. All counties. Resident.

*Everes comyntas* (Godart). Eastern Tailed Blue. DA,Ed,Gr,Hi. Resident.

*E. amyntula* (Boisduval). Western Tailed Blue. Be,Ca,Ci,Co,Gr,Li,LA,Lu,MK, Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*Celastrina argiolus echo* (W. H. Edwards). Spring Azure. All counties except Ch,Cu,DB,Gu,Ha,Qu,Ro,Va. Resident.

*Euphilotes battoides centralis* (Barnes and McDunnough). Buckwheat Blue. Be,Ca,Ci,Co,Gr,Li,MK,Ot,RA,Sv,SM,SF,Si,So,Ta,To. Resident.

*E. b. ellisi* (Shields). Ellis' Buckwheat Blue. SJ. Resident.

*E. enoptes ancilla* (Barnes and McDunnough). Dotted Blue. Co?,RA?,Sv,SJ, SF? Resident. Note 50.

*E. rita rita* (Barnes and McDunnough). Desert Buckwheat Blue. Ca,DA,Gr,Hi, Si,So. Resident.

*E. r. coloradensis* (Mattoni). Colorado Desert Buckwheat Blue. Sv, SF. Resident.

*E. r. emmeli* (Shields). Emmel's Buckwheat Blue. SJ. Resident.

*E. spaldingi* (Barnes and McDunnough). Colorado Plateau Blue. Ci,MK,RA, SJ,So,Ta,To. Resident.

*Glaucopsyche piasus daunia* (W. H. Edwards). Arrowhead Blue. Ci,MK,Sv,SJ. Resident.

*G. lygdamus oro* (Scudder). Silvery Blue. Be,Ci,Co,Li,LA,MK,Mo,RA,Sv,SJ, SM,SF,Ta,To,Un. Resident. Note 42.

*G. l. arizonensis* McDunnough. Arizona Silvery Blue. Ca,Gr,Si,So. Resident.

*Plebejus melissa melissa* (W. H. Edwards). Orange-Bordered Blue. All counties except Hi,Lu. Resident.

*P. saepiolus whitmeri* F. M. Brown. Greenish Clover Blue. Co,LA,Mo,RA,Sv, SJ,SM,SF,Ta. Resident.

*P. s. gertschi* dos Passos. Arizona Greenish Clover Blue. Ca. Resident.

*P. icarioides pembina* (W. H. Edwards). Rocky Mountain Lupine Blue. Ci,Co, Li,LA,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Ta,Un. Resident. Note 42.

*P. i. buchholzi* dos Passos. Mogollon Rim Lupine Blue. Ca,Gr,Si. Resident.

[*P. shasta* (W. H. Edwards)]. Hypothetical. Note 51.

*P. acmon texanus* (Goodpasture). Texas Emerald-Studded Blue. All counties. Resident.

*P. glandon franklinii* (Curtis). Arctic Blue. Be,Ca,Ci,Co,LA,MK,Mo,RA,Sv, SJ,SM,SF,So,Ta,To. Resident.


## RIODINIDAE (METALMARKS)

*Calephelis nemesis* (W. H. Edwards). Mexican Metalmark. DA,Gr,Hi. Resident.

*C. rawsoni arizonensis* McAlpine. Arizona Metalmark. Hi. Resident.

*Emesis zela* Butler. Southwestern Metalmark. Ca,Hi. Resident.

*E. ares* (W. H. Edwards). Chiricahua Metalmark. Hi. Resident.

*Apodemia mormo mormo* (C. and R. Felder). Mormon Metalmark. MK,RA, Sv,SJ,Ta. Resident.

*A. m. duryi* (W. H. Edwards). Dury's Metalmark. DA,Ed. Resident. Note 52.

*A. m. mejicana* (Behr). Mexican Mormon Metalmark. Be,Ca,Co,DA,Gr,Hi,Li, Lu,Ot,Sv,SF,Si,So,Ta,To. Resident.

*A. palmerii* (W. H. Edwards). Arizona Mesquite Metalmark. Be,Ca,DA,Gr,Hi, Li,Lu,Ot,So. Seasonal Resident.

*A. nais* (W. H. Edwards). Coppermark. Ca,Ci,Gr,LA,MK,RA,Sv,SM,SF, To. Resident.


## LIBYTHEIDAE (SNOUT BUTTERFLIES)

*Libytheana bachmanii larvata* (Strecker). Snout Butterfly. Be,Ca,Ch,Ci,Co, DB,DA,Ed,Gr,Gu,Ha,Hi,Le,Li,Lu,MK,Mo,Ot,Ro,SM,Si,Ta,To. Seasonal Resident.

[*L. carinenta* (Cramer)]. Hypothetical. Notes 2,53.

## NYMPHALIDAE (BRUSH-FOOTED BUTTERFLIES)

*Dione vanillae* (Linnaeus). Gulf Fritillary. Be,Co,DB,DA,Ed,Gr,Gu,Hi,Le,Li, Lu,Mo,Ot,Ro,Ta,Un. Seasonal Resident.

*D. moneta* Hubner. Mexican Silverspot. Ot. Stray.

*Heliconius isabella* (Stoll). Isabella Tiger. Ch. Stray.

*H. charitonius* (Linnaeus). Zebra Longwing. Be,Ch,Ed,Gr,Hi. Stray.

*Euptoieta claudia* (Cramer). Variegated Fritillary. All counties. Resident.

*E. hegesia* (Cramer). Mexican Fritillary. Hi,Lu? Stray.

*Speyeria cybele carpenterii* (W. H. Edwards). Great Spangled Fritillary. RA, Sv,SF,Ta. Resident. Note 54.

*S. aphrodite byblis* (Barnes and Benjamin). Aphrodite. Co,LA,Mo, SM,Ta,Un. Resident.

*S. nokomis nokomis* (W. H. Edwards). Seep Fritillary. Mo,SJ,SM,Ta. Resident. Note 55.

*S. n. nitocris* (W. H. Edwards). Arizona Seep Fritillary. Ca,Ci,Gr? Resident.

[*S. n. coerulescens* (W. Holland)]. Hypothetical. Note 56.

*S. edwardsii* (Reakirt). Green Fritillary. Co,RA,Sv,Un. Resident.

[*S. zerene* (Boisduval)]. Hypothetical. Note 57.

*S. atlantis nikias* (Ehrmann). Jemez Mountains Fritillary. LA,RA,Sv. Resident. Note 57.

*S. a. dorothea* Moeck. Sandia Peak Fritillary. Be,Ci,MK,Sv,SJ,To. Resident. Note 58.

*S. a. nausicaa* (W. H. Edwards). Gila Fritillary. Ca,Gr,Si,So. Resident.

*S. a. electa* (W. H. Edwards). Front-Range Fritillary. Co,Mo,RA,SM, SF,Ta. Resident.

*S. a. ratonensis* Scott. Raton Mesa Fritillary. Co. Resident. Note 59.

*S. a. capitanensis* R. Holland. Capitan Mountains Fritillary. Li,Ot. Resident. Note 60.

[*S. hydaspe* (Boisduval)]. Hypothetical. Note 61.

*S. mormonia eurynome* (W. H. Edwards). Mormon Fritillary. Be?,LA,MK,Mo, RA,Sv,SM,SF,Ta. Resident.

*Boloria selene tollandensis* (Barnes and Benjamin). Silver Meadow Fritillary. RA,Sv. Resident.

*B. freija browni* Higgins. Zigzag Fritillary. RA,Ta? Resident.

*B. titania helena* (W. H. Edwards). Purple Bog Fritillary. Co,LA,Mo,RA,Sv, SM,SF,Ta. Resident.

*Poladryas minuta minuta* (W. H. Edwards). Plains Penstemon Checkerspot. Co,Cu,DB,Gu,Ha,Mo,Qu,Ro,SM,Un. Resident.

*P. m. arachne* (W. H. Edwards). Montane Penstemon Checkerspot. Ca,Ci,Co, Gr,Li,MK,Mo,RA,Sv,SJ,SM,SF,Si,So,Ta,Un. Resident.

*Chlosyne theona thekla* (W. H. Edwards). Mexican Checkerspot. Ca,DA,Ed?, Gr,Hi,Li,Lu,Ot,Si,So. Resident

*C. t. bolli* (W. H. Edwards). Boll's Checkerspot. Cu. Stray.

*C. chinatiensis* (Tinkham). Chinati Mountains Checkerspot. Ed. Seasonal Resident.

[*C. cyneas* (Godman and Salvin)]. Hypothetical. Note 49.

*C. leanira fulvia* (W. H. Edwards). Orange Paintbrush Checkerspot. All counties except DB. Resident. Note 62.

*C. lacinia crocale* (W. H. Edwards). Sunflower Patch. Be,Ca,Ch,Cu,DA,Ed,Gr, Hi,Le,Li,Lu,MK,Ot,Ro,Sv,SF,Si,So,To,Va. Resident. Note 63.

*C. definita* (E. M. Aaron). Chihuahua Patch. DA,Ed,Lu,Ot,Si. Resident.

*C. janais* (Drury). Giant Patch. Ed. Stray.

*C. gorgone* (Hubner). Great Plains Checkerspot. Co,DB,Gu,Ha,LA,Mo,Qu,RA, Ro, Sv,SM,Un. Resident.

*C. nycteis drusius* (W. H. Edwards). Western Streamside Checkerspot. Ca,Co, Li,LA,Mo,Ot,RA,Sv,SM,SF,Ta,To,Un? Resident.

[*C. palla* (Boisduval)]. Hypothetical. Note 64.

*C. gabbii acastus* (W. H. Edwards). Pearly Checkerspot. Be,Ci,MK,RA,Sv,SJ, Ta. Resident.

*C. g. sabinus* (W. G. Wright). Southwestern Pearly Checkerspot. Ca,Gr,Lu,Si, So. Resident.

*Dymasia dymas* (W. H. Edwards). Tiny Checkerspot. Ca,DA,Ed,Gr,Hi,Lu,Ot, Si,So. Resident. Note 65.

*Texola elada ulrica* (W. H. Edwards). Ulrica Checkerspot. DA,Ed,Ro. Resident.

*T. e. perse* (W. H. Edwards). Perse Checkerspot. Ca,Gr,Hi,Lu. Resident.

*Phyciodes texanus texanus* (W. H. Edwards). Texas Crescent. Be,Ca,Ch,DB, DA,Ed,Gr,Hi,Li,Ot,Ro,Si,So,To. Resident.

[*P. tulcis* (H. W. Bates)]. Hypothetical. Note 2.

*P. vesta* (W. H. Edwards). Mesquite Crescent. DA,Ed,Gr,Gu,Hi,Ot,Qu,Ro,So, To? Resident.

*P. phaon* (W. H. Edwards). Mat-Plant Crescent. Cu,DB,Ed,Ro,Un. Resident.

*P. tharos tharos* (Drury). Pearl Crescent. Be,Ca,Ch,DB,DA,Ed,Gr,Gu,Ha,Hi, Lu,Mo,Ot,Qu,Ro,Sv,Si,So,Un,Va. Resident. Note 66.

*P. tharos* Type B. Orange Crescent. Ca,Co,Li,LA,Mo,Ot,RA,Sv,SJ,SM,SF,To, Un. Resident. Note 66.

*P. campestris camillus* W. H. Edwards. Field Crescent. All counties except Ch,Cu,DB,Gu,Le,Lu,Qu,Ro. Resident.

*P. pictus* (W. H. Edwards). Painted Crescent. All counties except Co,Cu,LA, MK,SF,To,Va. Resident. Note 67.

*P. mylitta callina* (Boisduval). Thistle Crescent. All counties except Ch,Cu, DB,Ed,Le. Resident.

*Euphydryas anicia capella* (Barnes). Capella Checkerspot. MK,RA,Sv,SJ,SM, Ta. Resident.

*E. a. chuskae* (Ferris and R. Holland). Chuska Mountains Checkerspot. SJ, MK. Resident. Note 68.

*E. a. cloudcrofti* (Ferris and R. Holland). Sacramento Mountains Checkerspot. Li,Ot. Resident. Note 69.

*E. a. eurytion* (Mead). Mead's Checkerspot. Co,RA,Ta. Resident.

*E. a. hermosa* (W. G. Wright). Hermosa Checkerspot. Ca,Gr,Hi. Resident.

[*E. editha* (Boisduval)]. Hypothetical. Note 70.

*Polygonia interrogationis* (Fabricius). Question Mark. Be,Ch,Co,Cu,DB,DA,
     Ed,Gr,Hi,Li,Ot,Ro,Sv,SM,SF,So,To,Va. Resident.

[*P. comma* (Harris)]. Hypothetical. Note 71.

*P. satyrus* (W. H. Edwards). Tawny Anglewing. Be,Ca,Ci,Co,DA,Gr,Gu,Ha,Hi,
     Li,LA,Lu,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*P. faunus hylas* (W. H. Edwards). Green Anglewing. Be,Co,Mo,RA,Sv,SM,SF,
     Ta. Resident.

[*P. silvius* (W. H. Edwards)]. Hypothetical. Note 70.

*P. gracilis zephyrus* (W. H. Edwards). Zephyr Anglewing. Be,Ca,Ci,Co,Gr,Li,
     LA,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*Nymphalis californica* (Boisduval). California Tortoiseshell. Ca,Ci,Gr,LA,RA,
     Sv,SJ,SM,SF,Si,To. Resident.

*N. antiopa antiopa* (Linnaeus). Mourning Cloak. All counties. Resident.

*Aglais milberti* (Godart). Fire-Rim Tortoiseshell. Ca,Ci,Co,Gr,Li,LA,Mo,Ot,
     RA,Sv,SJ,SM,SF,So,Ta,To. Resident.

*Vanessa virginiensis* (Drury). American Painted Lady. All counties. Resident.

*V. cardui* (Linnaeus). Painted Lady. All counties. Seasonal Resident.

*V. annabella* (Field). West Coast Lady. All counties except Ch,Cu,DB,Ed,Gu,
     Ha,Le,Qu. Resident.

*V. atalanta* (Linnaeus). Red Admiral. All counties. Resident.

[*Hypanartia lethe* (Fabricius)]. Hypothetical. Note 2.

*Precis coenia* (Hubner). Buckeye. All counties except Ci,Co,LA,Ta,To,Va.
     Resident.

*P. evarete nigrosuffusa* (Barnes and McDunnough). Dark Buckeye. Ca,DA,Ed,
     Gr,Hi,Lu,Va. Seasonal Resident.

*Anartia jatrophae luteipicta* Fruhstorfer. White Peacock. Ed. Stray.

[*Siproeta stelenes* (Linnaeus)]. Hypothetical. Note 72.

*S. epaphus* (Latreille). DA. Stray. Note 73.

*Limenitis arthemis arizonensis* W. H. Edwards. Arizona Red-Spotted Purple.
     Ca,DA,Ed,Gr,Hi,Li,Lu,Ot,Si,So. Resident.

*L. archippus archippus* (Cramer). Viceroy. Be,Gu,Ha,Mo,RA,Sv,SJ,SM,SF,So,
     Un,Va. Resident.

*L. a. obsoleta* W. H. Edwards. Desert Viceroy. Be,DB,DA,Ed,Gr,Hi,SJ,Si,So,
     Va. Resident.

*L. weidemeyerii* W. H. Edwards. Weidemeyer's Admiral. Be,Ca,Ci,Co,Gr,Li,
     LA,MK,Mo,Ot,RA,Sv,SJ,SM,SF,Si,So,Ta,To,Un. Resident.

*L. bredowii bredowii* (Geyer). California Sister. All counties except Cu,DB,Gu,
     Ha,Le,Qu,Un. Resident.

*Myscelia cyananthe* (C. and R. Felder). Dark Blue Wave. Ot. Stray.

*Eunica monima* (Stoll). Dingy Purplewing. Hi. Stray.

*Mestra amymone* (Menetries). Noseburn Wanderer. Ch,Ed,Hi,Le,Ro,So. Stray.

*Hamadryas februa* (Hubner). Gray Cracker. Hi. Stray.

[*Historis acheronta* (Fabricius)]. Hypothetical. Note 2.

[*Smyrna karwinskii* Geyer]. Hypothetical. Note 2.

[*Marpesia coresia* (Godart)]. Hypothetical. Note 74.

*M. petreus* (Cramer). Ruddy Daggerwing. Hi. Stray.

[*M. eleuchea* Hubner]. Hypothetical. Note 75.

*Anaea aidea* (Guerin-Meneville). Tropical Leafwing. Ch,Ed,Hi. Resident.

*A. andria* Scudder. Goatweed Butterfly. Be,Ca,Ch,Cu,DA,Ed,Gr,Gu,Ha,Hi,Le,
Li,Lu,Mo,Ot,Qu,Ro,Sv,SF,Si,Ta,To,Un,Va. Resident.

*Asterocampa celtis* (Boisduval and Leconte). Hackberry Butterfly. Be,Ca,Ch,
Co,Cu,DB,DA,Ed,Gr,Gu,Ha,Hi,Li,Lu,Mo,Ot,Qu,Ro,SM,Si,So,To,Un. Resident.

*A. leilia* (W. H. Edwards). Desert Hackberry Butterfly. Hi,Lu. Resident.

*A. clyton* (Boisduval and Leconte). Tawny Emperor. Ed,Gr,Hi,Lu. Resident.


## SATYRIDAE (SATYRS)

*Cyllopsis pyracmon henshawi* (W. H. Edwards). Henshaw's Satyr. Hi. Resident. Note 76.

*C. pertepida dorothea* (Nabokov). Nabokov's Arroyo Satyr. All counties except Cu,DB,Le,Ro,Qu,Va. Resident.

*Megisto rubricata rubricata* (W. H. Edwards). Red Satyr. Ch,Cu,DA,Ed,Gu, Ha,Li,Mo,Ot,Qu,SM,Un. Resident.

*M. r. cheneyorum* (R. Chermock). Southwestern Red Satyr. Ca,Gr,Hi, So. Resident.

*Coenonympha ochracea* W. H. Edwards. Ochre Ringlet. Be,Co,LA,Mo,RA,Sv, SM,Ta,To. Resident.

*Cercyonis pegala* (Fabricius). Large Wood Nymph. Be,Co,Cu,Gr?,Ha,Mo,Qu, RA,Ro,Sv,SJ,SM,SF,Ta,To,Un. Resident. Note 77.

*C. meadii meadii* (W. H. Edwards). Red Wood Nymph. SJ,RA. Resident. Note 78.

*C. m. mexicana* R. Chermock. Mexican Red Wood Nymph. Be,Ca,DA,Ed, Gr,Hi,RA,Sv,So,Ta,To. Resident. Note 78.

*C. sthenele paulus* (W. H. Edwards). Great Basin Wood Nymph. Ca?,SJ. Resident.

*C. oetus charon* (W. H. Edwards). Small Wood Nymph. Be,Ca,Co,Li,LA,Mo,Ot, RA,Sv,SJ,SM,SF,So,Ta,To,Un. Resident.

*Erebia magdalena magdalena* Strecker. Rockslide Alpine. Ta. Resident.

*E. epipsodea* Butler. Common Alpine. Mo,RA,SM,SF?,Ta. Resident.

[*E. callias* W. H. Edwards]. Hypothetical. Note 79.

*Gyrocheilus patrobas* (Hewitson). Red-Bordered Brown. Ca,Gr,Hi,Si. Resident.

*Neominois ridingsii ridingsii* (W. H. Edwards). Ridings' Satyr. Co,Gu,Mo,RA, SM,Ta,Un. Resident.

*N. r. neomexicanus* Austin. New Mexico Satyr. Ca,Ci,MK. Resident. Note 80.

*Oeneis chryxus chryxus* (Doubleday and Hewitson). Chryxus Arctic. Co,LA, Mo,RA,Sv,SM,SF,So,Ta. Resident. Note 81.

*O. uhleri uhleri* (Reakirt). Uhler's Arctic. Co,RA,Ta. Resident.

*O. alberta capulinensis* F. M. Brown. Capulin Mountain Arctic. Co, Un. Resident. Note 82.

*O. a. daura* (Strecker). Mogollon Rim Arctic. Ca. Resident.

*O. melissa melissa* (Fabricius). Mottled Arctic. Mo,RA,Ta. Resident.

*O. polixenes brucei* (W. H. Edwards). Banded Arctic. Mo,RA,SF,Ta. Resident.

## DANAIDAE (MILKWEED BUTTERFLIES)

*Danaus plexippus* (Linnaeus). Monarch. All counties. Seasonal Resident.

*D. gilippus strigosus* (H. W. Bates). Desert Queen. All counties except Va. Resident.

*D. eresimus* (Cramer). Soldier. Hi. Stray.

## NOTES

1. A specimen in the USNM is labeled "N. Mex.", which probably refers to northern Mexico.

2. This is an Edwards (1872) report, without supporting data or specimens.

3. A 1982 report from the Guadalupe Mountains, Eddy Co., is based on a sight record and requires confirmation.

4. There are two old NM reports of this non-migratory Great Plains species. One specimen, collected in 1882 by F. H. Snow near Las Vegas, San Miguel Co., was examined by Toliver and found to be *T. pylades*. The other is an AMNH specimen allegedly collected by Cohn in 1951 near Jemez Springs, Sandoval Co. Assuming a correct identification (determined by Stanford in 1971), the specimen may be mislabelled or it may have been brought into NM as an immature in livestock forage.

5. One 1899 sight record by Cockerell from Dona Ana Co. is unsupported because of difficulty identifying *clitus* in hand, let alone in flight. The NMSU collection contains a ca. 1900 Townsend specimen from Dona Ana Co. catalogued under *E. j. clitus*; Cary examined it and found it to be *E. tristis tatius*.

6. Snow's 1882 specimen from Las Vegas, San Miguel Co., was examined by Toliver and found to be *E. telemachus*.

7. Williams claimed this taxon from the Jemez Mountains, April -June 1913. Flight period and resemblance to *E. telemachus* suggest misidentification of the latter, which is common there, yet went unreported by Woodgate or Williams. A report of *propertius* from the Sandia Mountains in 1959 by Stallings, Turner and Ehrlich ("1959"[1960]) probably has a similar explanation. Until *E. telemachus* was described by Burns in 1960, observations of *telemachus* were erroneously assigned to other taxa.

8. Plate 93 in Howe (1975) illustrates a Colfax Co. specimen of *E. horatius* incorrectly captioned as *E. meridianus*. Toliver examined the actual specimen and noted the error.

9. One old specimen is labelled "Alamo, NM". The only such place is a highway intersection in eastern Guadalupe Co. Although within the range of *E. horatius*, no other butterfly reports are known from there. The specimen likely originated from Alamogordo, Otero Co., which experienced much butterfly collecting ca. 1900 and whose Sacramento Mountains support abundant *E. horatius*. Local residents casually refer to Alamogordo as Alamo. "Alamo" is Spanish for cottonwood tree.

10. All six reports of this species from NM are suspect. Snow (1883) reported *E. martialis* from Water Canyon, Socorro Co. Toliver examined the specimen and found two errors: it was *E. horatius* and it was labelled Gallinas Canyon, San Miguel Co. A report by Stallings, Turner and Ehrlich ("1959"[1960]) from the Sandia Mountains is probably *E. telemachus* (see Note 7). The remaining four are Carl Cushing reports from the Jemez Mountains in the mid-1960s. This is the most likely place to find *E. martialis* in NM, but neither Woodgate's many years of collecting there nor Holland's recent survey turned it up. Cushing's reports may be *E. horatius* or *E. telemachus*.

11. Difficulty distinguishing *E. persius* from *E. afranius* has lead to several unverifiable determinations of NM specimens.

12. Some argue that *P. c. communis* and *P. c. albescens* can be separated based on genitalic differences and are therefore separate species. Other lepidopterists (e.g., Scott, 1986) believe they represent one genitalically dimorphic taxon. Bailowitz and Brock (1991) report genitalic intergrades in southeast AZ. Although we have not examined genitalia of NM specimens, we know of no place in NM where *P. c. albescens* occurs in the absence of *P. c. communis*. We believe they may be conspecific, with *P. c. albescens* more common at lower altitudes and toward AZ.

13. The type locality of *H. alpheus*, described in 1876, is southwest of Raton in Colfax Co.

14. This skipper is named for John Woodgate, who collected the type specimens in the Jemez Mountains in 1913.

15. *H. viridis* was described in 1883 from specimens collected by Snow near Las Vegas, San Miguel Co. Snow first reported these specimens as *H. juba*.

16. A 1968 report from Capulin Mountain National Monument, Union Co., was examined by Toliver and found to be *P. origenes*.

17. Form *stigma* (Skinner), now a synonym of *P. vibex brettoides* (W. H. Edwards), was described in 1896 from material collected in "southern NM". No other NM reports of *P. vibex* are known. The LACM has an old, properly catalogued specimen of *H. phyleus* with an old label calling it "*brettoides*". This suggests misidentification in the past, made possible because males of *P. vibex* and *H. phyleus* are quite similar. Females are easy to tell apart, but Skinner's description of *stigma* includes no females! We suggest that the types of *stigma* may actually be *H. phyleus*. The types of *stigma* should be examined and their identity resolved.

18. Evans' (1955) reference to a NM specimen in the British Museum requires substantiation.

19. Snow reported this from Gallinas Canyon, San Miguel Co., in 1882. This must be either an aberrant or a misidentified *P. taxiles*, which is common there. Similarity between these two taxa is indicated by Scott's (1986) opinion that they are conspecific, an opinion we do not share. *P. taxiles* was described in

1881; Snow was probably unaware of the existence of this new western *Poanes* at the time of his NM report.

20. Snow reported this from Gallinas Canyon, San Miguel Co., in 1882. This must be a misidentification of *E. vestris*, which is common there.

21. Henry L. Viereck collected the type specimens of *A. vierecki* from Dry Canyon near Alamogordo, Otero Co., May 8-13, 1902.

22. Form *margarita* (Skinner) was named in 1914 from specimens collected by Woodgate near Jemez Springs, Sandoval Co.

23. In 1981 Cibola Co. was created from the western part of Valencia Co. Pre-1981 Valencia Co. reports lacking detailed locality data are now impossible to attribute to either present-day Valencia or Cibola counties. *A. oslari* is one species with such a report.

24. In 1911 Skinner described *Pamphila quinquemacula* from Las Cruces, Dona Ana Co. It is synonymous with *A. eos*.

25. There is one report of this species from Jemez Springs, Sandoval Co. It must be a misidentified *A. phylace*, which is common there and very similar in appearance. The closest occurrence of *A. fimbriata* is in the Chiricahua Mountains of southeast AZ, about 500 km distant.

26. D. Stallings and Turner described *A. carlsbadensis* in 1957 from Carlsbad Caverns National Park, Eddy Co. Taxonomists consider this to be either a synonym or a subspecies of *A. neumoegeni*.

27. The numerous named populations of this taxon need work. In 1911, *M. y. navajo* Skinner was described from Ft. Wingate. McKinley Co. *M. y. elidaensis* D. Stallings, Turner and J. Stallings was described in 1966 from Elida, Roosevelt Co.

28. *M. u. violae* D. Stallings and Turner, synonymized by Scott (1986), was described in 1956 from specimens collected at Carlsbad Caverns National Park, Eddy Co.

29. Rincon, NM, is the type locality of *P. p. curvifascia* (Skinner), described in 1902 and now part of the synonymy. Where is Rincon? The word means "corner" or "box canyon" in Spanish, and is common in the NM toponymy. Pearce (1965) discusses 10 such places in NM, a small fraction of the total. The railroad junction at Rincon, in Dona Ana Co., is the most likely origin of *P. p. curvifascia*.

30. Published reports of *P. bairdii* from Otero and Lincoln counties were re-examined by the authors and determined to be *P. polyxenes*. Several Sierra and Socorro county reports were similarly dismissed. A single alleged *P. bairdii* capture from Grant Co. was considered uncertain by the collector.

31. Visual sightings of *P. cresphontes*, indicated by "?", may refer to the very similar, but less common, *P. thoas*. All known specimens from NM are *P. cresphontes*.

32. *P. eurymedon* is one of several species with dubious old reports from High Rolls, Sacramento Mountains, Otero Co. The others are *S. sylvinum*, *C. fotis*, *O. chryxus*, and *S. behrii*, all species for which no confirmed records exist for the Sacramento Mountains or any other place within a 300-km radius. Necessary habitat and larval hostplants are limited or absent, and none are known to wander.

33. Edwards (1872) attributes *P. pilumnus* to NM, but without substantiating data. Bailowitz and Brock (1991) cite some AZ records, so it may turn up here

some day. AZ Territory was not formally separated from NM Territory until 1863, so NM reports from Edwards' era and earlier may actually be from localities now within the State of Arizona.

34. Cushing reports two Luna Co. localities (Columbus and Deming) for this species, but no specimens have been examined. Misidentification of the similar *B. philenor*, which breeds there, is the most plausible explanation for these reports.

35. Most specimens from southwestern Hidalgo Co. tend toward form *transversa* Barnes and Benjamin, now dubiously synonymized with *P. sisymbrii*.

36. This species is uncommon in NM, limited to the highest peaks. Taxanomic confusion with the ubiquitous and weedy *P. protodice* has lead to unconfirmed reports of *P. occidentalis* from Colfax, Rio Arriba, Sandoval and San Miguel counties.

37. *P. napi mogollon* was named in 1942 for the Mogollon Mountains of Catron Co., where some of the types were collected.

38. Specimens resembling *A. s. inghami* Gunder are most common in southwest NM, while the *A. s. julia* W. H. Edwards phenotype prevails in northern NM.

39. Subspecies *ruckesi* was described in 1937 from specimens collected near Cowles in San Miguel Co.

40. Ehrlich and Ehrlich (1961) depict an alleged NM *E. salome*, but no specimens with data are known. Cary reported one from Hidalgo Co. in 1984, but Bailowitz examined it and determined it to be *E. boisduvalianum*.

41. In 1882 Snow reported *Chrysophanus ianthe* (W. H. Edwards), now *L. nivalis*, from Gallinas Canyon, San Miguel Co. In 1966 R. Langston reported it from the Jemez Mountains, Sandoval Co. Both must be misidentifications.

42. The small population in the Sacramento Mountains may warrant description as a separate taxon.

43. *C. spinetorum* is dimorphic in southcentral NM. The less common form resembles *C. millerorum* (Clench), which was described in 1981 from Mexico. Robbins (1990) showed that, despite two forms, only one species is present in Otero Co.

44. *C. g. siva* was described in 1874 from specimens collected at Ft. Wingate, McKinley Co. In southeast NM, this taxon appears to interbreed with *C. g. gryna*. Specimens with some wing characters of nominotypical *gryna* are known from Chaves, Colfax, Eddy, Otero, Quay and Taos counties.

45. This species was described in 1960 from specimens collected in the Sandia Mountains near Albuquerque.

46. "New Mexico" is the type locality for *C. a. annetteae* (dos Passos), which was described in 1947 and is now dubiously synonymized.

47. The type locality of *F. f. violae* (D. Stallings and Turner) is near Folsom, Union Co. It was described in 1947 and is now synonymized.

48. *F. p. organensis* Ferris was described in 1979 from the Organ Mountains in Dona Ana Co. It was synonymized by Scott (1986).

49. A single unsubstantiated report requires confirmation.

50. *E. enoptes* is apparently rare in NM. Perhaps two valid records are known. Reports from Santa Fe, Colfax and Rio Arriba counties are suspect and require confirmation.

51. A vague reference to Taos Co. for this species is on file, but we know of no specimens or data to support it.

52. Populations of *A. mormo* in NM do not conform well to the named subspecies available. *A. m. duryi* is very distinct and may be a full species; it was described in 1881 from near Mesilla, Dona Ana Co.

53. Cary reported it twice, but his were misidentifications based on the incorrect figure in Howe (1975).

54. *S. c. carpenterii* was described in 1876 from specimens collected by the Wheeler Expedition to NM. In 1947 the type locality was fixed as Taos Peak, Taos Co.

55. Form *S. n. nigrocaerulea* (W. and T. Cockerell) was described in 1900 from Sapello Canyon, San Miguel Co. It has been synonymized variously with *S. n. nokomis* and *S. n. nitocris*. Aberration *S. n. rufescens* (T. Cockerell) was described from the same location in 1909.

56. Subspecies *S. n. coerulescens* is a puzzle in NM. There are two old reports of *S. nokomis* from Otero Co., but most of the habitat there has been destroyed and recent attempts to locate colonies have failed. Thus there is no way to confirm the old reports. If *nokomis* is or was there, it may or may not be this Mexican race.

57. There is no evidence that *S. zerene* occurs in NM, despite recent references to the contrary (e.g., Tilden and Smith, 1986), which perpetuate outdated information. Williams (1914) reported *zerene* among Woodgate's material, but this cannot be taken at face value. Williams did not report *S. atlantis*, an unusual omission because it is abundant there and Woodgate provided the type material for *S. a. nikias* (Ehrmann). Ehrmann (1917), however, in his description of *nikias* from Temez [sic] Springs, includes the following revelation: "when I received this species of *Argynnis* [now *Speyeria*] from Mr. John Woodgate he wrote me: 'This species has been identified by two different authorities, one named it *Arg. bremneri* Edw. and the other, *Arg. behrensi* Edw.'" Both identifications offered to Woodgate are now recognized as subspecies of *S. zerene*, hence Williams' report. Ehrmann recognized its distinctness, however, and gave it a new name which is now treated as a subspecies of *S. atlantis*.

58. Subspecies *S. a. dorothea* was described in 1947 from the Sandia Mountains, Sandoval Co.

59. Subspecies *S. a. ratonensis* was described in 1981 from specimens collected on Raton Mesa, Colfax Co.

60. Subspecies *S. a. capitanensis* was described in 1988 from the Capitan Mountains, Lincoln Co.

61. *S. hydaspe conquista* dos Passo and Grey was described in 1945 from material allegedly collected on August 8, 1932, near Santa Fe. Other specimens were allegedly taken four days later near Therma, now Eagle Nest, in Colfax Co., and one of these specimens is figured by Howe (1975, Plate 31, figure 15). No one has seen this species anywhere in NM before or since. We believe these specimens were actually collected elsewhere, perhaps Wyoming, and mislabelled.

62. NM material has been variously assigned to the genera *Chlosyne* and *Thessalia*, and to such species as *leanira* (C. and R. Felder), *alma* (Strecker)

and *fulvia*. A 1988 revision added subspecies *C. l. coronado* (M. Smith and Brock) to the names available. Because *C. leanira* occurs statewide, is unrestricted by major physiographic barriers, and is variable, we place all NM populations into one taxon, *fulvia*.

63. In 1893 W. H. Edwards named several forms of *C. l. crocale* from near Las Cruces, including *rufescens* and *nigrescens*.

64. In the AMNH there is an old specimen of *C. palla* labelled Jemez Springs. It is either mislabelled or misidentified.

65. Individuals resembling AZ subspecies *D. d. chara* (W. H. Edwards) occur in southwest NM and intergrade with the nominate phenotype which prevails to the east.

66. Populations formerly thought of as *P. tharos* actually represent at least two species, perhaps as many as four (Ferris, 1989). In addition, the nomenclature is in disarray. We recognize two taxa at this time, calling them *P. tharos* and *P. tharos* Type B until better names are provided.

67. Aberration *jemezensis* Brehme was bred by Woodgate in 1912 in Jemez Springs, Sandoval Co.

68. The type locality of *E. a. chuskae* is the Chuska Mountains of San Juan Co.

69. The type locality of *E. a. cloudcrofti* is the Sacramento Mountains near Cloudcroft, Otero Co.

70. The INHS has in its collection a specimen labelled Las Vegas, NM. However, Toliver determined that it was purchased, not collected, in Las Vegas.

71. Common eastern *P. comma* is misrepresented in NM by one old Skinner report from San Miguel Co. It is either mislabelled, misidentified, or else it came in on the train.

72. There are no documented reports of this species from NM. There is an unsubstantiated report by Edwards (1872). R. Holland caught one 2 mi. south of the NM/TX border. Bailowitz and Brock (1991) report one sighting from AZ.

73. *S. epaphus* is not listed in Scott (1986), Miller and Brown (1981), or revisions thereto. Paul Opler found this NM and US record in the Oregon State University collection.

74. Edwards (1872) lists this species from NM, but without supporting data. Howe (1975) figures a specimen from El Paso, TX, just south of the NM border.

75. Scudder (1892) reported this species from NM without supporting data.

76. Some authors present this taxon as two separate species: *C. pyracmon* (Butler) and *C. henshawi* (W. H. Edwards). We believe they are seasonal forms of the same species. Otero Co. reports are erroneous, probably mislabbeled as to locality.

77. NM specimens do not fit well within subspecific taxa available. Some resemble *C. p. texana* (W. H. Edwards), while others resemble Rocky Mountain populations sometimes assigned to *C. p. boopis* (Behr). Scott (1986) places our populations with *C. p. nephele* (W. Kirby).

78. *C. meadii* is variable, and variation in NM specimens is not captured by the subspecific names available.

79. Holland (1905, pp. 209-210) claims it is "not uncommon on the high mountains of New Mexico." We know of no actual specimens or records with data.

80. The type locality of *N. r. neomexicanus*, described in 1986, is the Zuni Mountains of west-central NM.

81. An isolated colony of *O. chryxus* in the San Mateo Mountains, Socorro Co., may warrant subspecies status.

82. *O. a. capulinensis* was described in 1970 from Capulin Mountain National Monument in Union Co.

## LITERATURE CITED

BAILOWITZ, R. A., & J. P. BROCK, 1991. Butterflies of southeastern Arizona. Sonoran Arthropod Studies, Inc. Tucson. 342 pp.

EDWARDS, W. H., 1872. Synopsis of North American butterflies. American Entomological Society. Philadelphia. 52 pp.

EHRLICH, P. R., & A. H. EHRLICH. 1961. How to know the butterflies. W. C. Brown Co. Dubuque, IA.

EHRMANN, G. A., 1917. Some new North American butterflies. Lepidopterist 1:54-56.

EVANS, W. H., 1951-1955. A catalogue of the American Hesperiidae in the British Museum (Natural History), in 4 parts. The British Museum (N.H.). London.

FERRIS, C. D., 1989. Supplement to: a catalogue/checklist of the butterflies of America north of Mexico. The Lepidopterists' Society. Memoir No. 3. 103 pp.

FERRIS, C. D., & F. M. BROWN, 1981. Butterflies of the Rocky Mountain states. U. of Oklahoma Press. Norman. 442 pp.

HOLLAND, W. J., 1905. The butterfly book: a popular guide to a knowledge of the butterflies of North America. Doubleday, Page & Co. New York. 382 pp.

HOWE, W. W., 1975. The butterflies of North America. Doubleday & Co., Inc. Garden City, NY. 633 pp.

MILLER, L. D., & F. M. BROWN, 1981. Catalogue/checklist of the butterflies of America north of Mexico. The Lepidopterists' Society. Memoir No. 2. 280 pp.

PEARCE, T. M., 1965. New Mexico place names: a geographical dictionary. U. of New Mexico Press. Albuquerque. 187 pp.

ROBBINS, R. K., 1990. The *Mitoura spinetorum* complex in New Mexico and the validity of *M. millerorum* (Lycaenidae:Theclinae). J. Lep. Soc. 44(2):63-76.

SCOTT, J. A., 1986. The butterflies of North America; a natural history and field guide. Stanford U. Press. Stanford, CA. 583 pp.

SCUDDER, S. H., 1892. The tropical faunal element of our southern Nymphalinae, systematically treated. Proc. Am. Acad. Arts and Sci.:236-251.

SNOW, F. H., 1883. List of Lepidoptera and Coleoptera collected in New Mexico by the Kansas University scientific expedition of 1881 and 1882. Trans. Kan. Acad. Sci. 8:35-45.

STALLINGS, D. B., J. R. TURNER, & P. R. EHRLICH, "1959"(1960). A "hit and run" trip to Texas and New Mexico. J. Lep. Soc. 13: 99-100.

TILDEN, J. W., & A. C. SMITH, 1986. A field guide to western butterflies. Houghton Mifflin Co. Boston. 370 pp.

TOLIVER, M. E., & R. HOLLAND, 1977(1992). Distribution of butterflies in New Mexico (Lepidoptera: Hesperioidea and Papilionoidea). R. Holland (ed.). 1st ed. Albuquerque. 232 pp.

WILLIAMS, R. C., 1914. One hundred butterflies from the Jamez [sic] Mountains New Mexico (Lepid.). Ent. News 25:263-268.

# A survey of the Lepidoptera fauna from the Blue Mountains of eastern Oregon

David G. Grimble and Roy C. Beckwith

Pacific Northwest Research Station, USDA Forest Service, Forestry Sciences Laboratory, Corvallis, Oregon 97331 USA

and

Paul C. Hammond

Department of Entomology, Oregon State University, Corvallis, Oregon 97331 USA

**Abstract**. Blacklight trap and aerial net collections for 1 season resulted in identification of 55 species of day-flying Lepidoptera and an additional 383 species of moths in northeastern Oregon mixed-coniferous forests. A total of 212 moth species (55%) were Noctuidae and an additional 93 species (24%) were Geometridae. Notes are presented on the relative abundance of moths in trap collections, flight period of trapped moths, and larval host food plants. Most species were represented in trap collections by few individuals; 41.5% had 5 or fewer specimens, and an additional 30% had 25 or fewer specimens. Only 5.5% of the species were considered abundant, with 200 or more specimens trapped.

## INTRODUCTION

The Blue Mountains of eastern Oregon are characterized by moderate slopes, relatively low annual precipitation, and high summer temperatures (Franklin and Dyrness 1988). Higher elevation sites are usually occupied by mixed-coniferous forests of predominately ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, grand fir, *Abies grandis* (Dougl.) Lindl., and western larch, *Larix occidentalis* Nutt. However, stream bottoms, spring-fed marshy areas, and other riparian zones usually contain a variety of hardwood shrubs, forbs, and grasses. Historically, major outbreaks of forest insect defoliators (e.g. western spruce budworm, *Choristoneura occidentalis* Free., and Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunn) have occurred in this region, resulting in large aerial spray suppression programs (Brookes et al. 1978; Brookes et al. 1987). Similar outbreaks will happen again in the future. Thus, the Blue Mountains are of special interest to Oregon forest managers who are concerned with protecting forests from unacceptable insect damage.

When damaging outbreaks of forest defoliators do occur, microbial insecticides are preferred for suppression of the insect populations because of their insect selectivity, high degree of environmental safety, and general public acceptance. Since 1980, *Bacillus thuringiensis* Berliner subsp. *kurstaki*, (BTK), has been the microbial insecticide of choice for most forest spraying in the United States and Canada. Although BTK

is a lepidopterous disease agent, its relative safety has been determined
for many organisms in the environment, such as birds, fish, mammals,
some non-lepidopterous insects and other arthropods (e.g. Eidt 1985;
Niwa et al. 1987; Kreig and Langenbruch 1981). Still, questions fre-
quently arise about whether or not desirable moths and butterflies in the
spray area may be decimated along with the target species. In a study
related to a gypsy moth, *Lymantria dispar* (L.), suppression program
using BTK in oak stands in western Oregon, Miller (1990) found that
overall abundance and species richness was reduced among 35 species in
10 lepidopterous families. In that instance, however, BTK was sprayed
3 times in 1 season over the same acreage. For western spruce budworm
or Douglas-fir tussock moth suppression, the norm is only 1 spray per
year with many years interval before that suppression is again neces-
sary. In a later study, Miller (1992) found that a single BTK treatment
caused an immediate significant reduction in nontarget larval abun-
dance, which was still noticeable the following season. He observed that
species richness decreased among the less-abundant (or uncommon)
species on the spray site--perhaps eliminating them from the system--and
that effects on species richness and abundance might be masked by
examination of only the gross results of spraying on the more common
species. He stated that this potential danger to uncommon species on the
spray site justifies special management consideration to protect rare or
endangered species. This, of course, presupposes that management
knows what rare or endangered species are present, a condition that can
only be met by adequate baseline surveys prior to treatment.

With the prospect of continued or increasing use of BTK for forest
protection in the future, it is essential that we learn more about the
unintended impacts of broad-scale BTK sprays. The first requirement for
that is to know as precisely as possible the diversity and relative
abundance of species present before treatment. No comprehensive inves-
tigation of the effects of BTK sprays on nontarget Lepidoptera has yet
been done in Blue Mountains mixed-coniferous forests, although it is
known that many species of Lepidoptera exist in areas sometimes
sprayed (Forsberg et al. 1976). Cumulative lists of Lepidoptera have been
compiled and maintained for areas west of the Cascade Mountains crest
(e.g. Parsons et al. 1991), but similar survey lists are not available for the
Blue Mountains. The insect fauna of eastern Oregon is different from
that of more mesic western areas. This paper reports the results of an
initial survey to gather baseline data necessary to evaluate the impacts
of BTK sprays on nontarget Lepidoptera present on potential spray sites
in the Blue Mountains.

## METHODS

In 1992, we operated ULV blacklight traps at 4 locations in the Blue Mountains
between LaGrande, in Union County, and Ukiah, in Umatilla County, Oregon.
Paired research plots were established in the Wallowa-Whitman National Forest

and the Umatilla National Forest. Plots 1 and 2 were spaced about 1 km (0.625 mi.) apart along Meadow Creek on Starkey Experimental Forest (Sec. 35 and 27, T.3 S., R.34 E.). Plots 3 and 4 were at 1 km intervals in the upper watershed of Pearson Creek and at Granite Meadow (Sec. 25 and 35, T.3 S., R.32 E.), both about 10 km west of Meadow Creek. Meadow Creek has year-around running water, while both of the other areas are spring-fed, marshy sites where surface water often dries up in midsummer. All 4 plots had similar riparian vegetation and woody plants present, as well as a wide variety of grasses and forbs. All were subject to cattle grazing, although plot 1 on Meadow Creek had some fenced portions to exclude cattle.

Two ULV blacklight traps were placed in each plot during the first week of May. Traps were universal-type (BioQuip Products Inc.[1]), with circular 22-watt flourescent blacklight bulbs powered by 12-volt auto batteries. Vapona®[1] insecticide strips were placed in the lower trap sections to act as killing agents for trapped insects. A photoelectric switch in each trap allowed automatic dusk-to-dawn operation. Traps were hung from individual tree branches, about 1.5 m from the ground, in positions unobstructed from view by tree branches. Except for the last week of August and a 2-week period in mid-September, the traps were operated for 3 consecutive nights each week until October 10. Moths were collected daily from traps and taken to the laboratory for later identification.

Day-flying species, primarily butterflies, were sampled by frequent, brief net collections in plots after the traps had been serviced.

All macrolepidoptera were identified to species, but only part of the microlepidoptera could be identified; these were primarily the larger species in the families Pyralidae and Tortricidae. Species of Pterophoridae were attracted to the blacklight traps, but were not identified. Very small moths of the gelechioid families were not considered in this study. Voucher specimens of species discussed in this paper are stored at Forestry Sciences Laboratory, Pacific Northwest Research Station, Corvallis, Oregon.

## RESULTS AND DISCUSSION

A total of 54 species of butterflies and 1 day-flying Arctiidae were collected at the 4 trapping sites (Table 1), which probably represents most, but not all, of the day-flying lepidopteran species. All of these species had been previously taken in Oregon (Dornfeld 1980; McFarland 1963; Parsons et al. 1991). No attempt was made to collect all individuals available—only a representative sample of the species active at the time. The intent was to document species richness, but not abundance, since available time did not allow systematic net sampling. The 1992 field season began as an "early spring." Some species may have been missed or were well into their flight period by the time our collections began. Had we started earlier than the first week of May, it is likely that we would have caught more individuals of certain species (those with overwintering adults, or early emergence), or even additional species. By the final

[1]The use of trade names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

week of sampling (October 7), night temperatures were often below freezing, days were usually cool, and the flight period for most Lepidoptera was clearly over.

Two families (Nymphalidae, Lycaenidae) account for well over half (35) of the total species collected. These are often some of the most abundant butterflies active and feeding on flowers on any particular day. Larval hosts for most of the species in Table 1 are primarily various flowering plants, such as violets, lupines, and thistles. Hardwood shrubs (e.g. willow, blueberries) are also common food sources in spring. Still, there are guilds of satyrids and hesperiids which feed as larvae on grasses.

Two species in Table 1 were not actually captured by net. Because the adults typically fly around and rest in the tops of pine trees infested by their host plants, *Mitoura spinetorum* (Hewitson) larvae were collected from dwarf mistletoe plants (*Arceuthobium campylopodum* Engleman) on pines and reared to the adult stage. Similarly, larvae of *Satyrium sylvinus* (Boisduval) were found on willow leaves and reared to adults.

Larvae of the arctiid moth *Gonophaela vermiculata* (Grote) were collected in May and reared to adults on their food plant tall bluebells, *Mertensia paniculata* (Ait.) G. Don, and later taken by net from the same host. This moth is not active at night and none of these were caught in light traps.

Table 2 shows the complete list of all 383 species of moths taken in blacklight traps over the May-October period. Of these, 55% (212 species) were noctuids; the genus *Euxoa* alone was represented by 37 species. Geometridae was the second largest family, with 93 species identified. The total number of individuals of each species caught is given only to indicate relative abundance, as these data were subject to influence by other factors, such as the behavioral characteristics of the individual species (e.g. some species may not respond well to the specific wavelength of the ULV lights). Still, some species seemed to be especially abundant. For example, we collected 2205 *Spilosoma vagans* (Boisduval), 2033 *Petrophila confusalis* (Walker), and 1075 *Euxoa munis* (Grote).

Conversely, the data in Table 2 show that a large number of species apparently have sparse populations or are poorly attracted to ULV lights. For many species, we caught only 1 to 3 specimens, all in the same week. When this single-instance catch happened during the first week of trapping (May 6), e.g. *Cladara limitaria* (Walker) or *Behrensia conchiformis* Grote, it may represent catch at the end of the flight period. Earlier trapping might have resulted in more individuals of these species being caught. However, when we trapped a single specimen (or even 2 or 3) during only 1 week later in the season, e.g. *Alucita hexadactyla* Linnaeus or *Malacosoma californicum* (Packard), that may be the result of an actual paucity of individuals available to be caught. Also, there is some evidence (unpublished data) that many species do not disperse far from their food plants or pupation locations and thus may not reach the traps in quantities truly representative of their population density.

A comparison of the relative abundance of the different species, based solely upon the total numbers of individuals per species caught during the whole season (Table 3), shows that the vast majority of species (273 of 383) may indeed have quite sparse populations. We caught 5 or less individuals in 159 species, and 25 or less in an additional 114 species. To be ranked as rare or uncommon species, the criteria of 25-or-less specimens trapped over the season should be a conservative goal. Assuming only a 2-week emergence and dispersal period, that usually would allow for 12 trap-nights per site (2 weeks/2 traps/3 nights) in which to catch 25 moths, an easily attainable number since few species were restricted to only 1 pair of traps. The majority of rare or uncommon species were in the Noctuidae (60%). Conversely, only 5.5% (21) of all species could be considered abundant, as indicated by a total catch of 200 or more individuals.

Because the net collections did not systematically sample populations of day-fliers (Table 1), no direct comparison of relative abundance by species can be made. Nevertheless, some genera of butterflies were noticeably abundant on warm days, such as *Polites* sp., *Pyrgus* sp., *Icaricia* sp., *Lycaena* sp., *Speyeria* sp., and *Vanessa* sp.

Ten of the species listed in Table 2 were new records for Oregon (Grimble et al. 1993) and an additional 18 species had previously been collected in Oregon only from the western mountain ranges (both groups identified by footnotes).

Some species, for example *Scoliopteryx libatrix* (Linnaeus) and 3 species of *Xylena*, are known to overwinter as adults. Examination of the flight period data in Table 2 leads to the conclusion that many other species probably also have at least some adults overwintering, as well as some producing more than 1 generation per year. For instance, *Epirrita autumnata* (Borkhausen) was trapped in early June; then, no specimens were taken until late September. Examples of species caught over a 6-8 week period, or longer, are numerous, such as *Spilosoma vagans* (Boisduval) and *Sphinx vashti* Strecker. This extended flight period may be the result of microclimatic variation in pupation sites.

Where host plants are known, the larvae of most species tend to utilize angiosperms as food sources. Many of them apparently develop equally well on a range of food plants, such as herbs and hardwoods. Some, on the other hand, have been usually collected from only one host plant; e.g. *Semiothisa denticulata* (Packard) and *S. sexmaculata* (Packard) on larch or tamarack (*Larix* sp.). A summary of the number of species known to use certain host plant types (Table 4), shows that hardwood trees and shrubs (44%), and herbs, and grasses (43%) make up most of the food. Conifers make up a distant third preference (10%), even though eastern Oregon forests are nearly pure coniferous types. Evidently, Lepidoptera find much of their food in moist, riparian zones where hardwoods, grasses, and herbs are more abundant. Few species (2%) alternate between conifers and hardwoods.

The baseline data presented in this paper probably represent the majority of butterfly species and a large portion of the moth species present in our study areas. The number of moth species may be underestimated, partly because some species are not readily attracted and caught in blacklight traps. Thus, the fact that low numbers of certain species were collected in traps may not be truly indicative of their rarity.

These data will be useful when decisions are made concerning the impacts of BTK on nontarget Lepidoptera. However, such decisions must also be based upon the biology of larvae of the species in question. Clearly, a species must be present in larval form at the time of spraying to be impacted by the spray. Our baseline data will help managers determine which species fit into this category. Furthermore, Peacock and Schweitzer (1993, in press) made it clear that early instars of a species are generally more susceptible to BTK than are later instars. Still, this is not always the case, and it appears that BTK susceptibility must be considered on a species-to-species basis.

Additional field work is needed to document the larval and flight periods of species on our study areas, particularly those which may be "rare," "uncommon," or otherwise of "special concern." Many species of Lepidoptera contribute significantly to the food resources of other wildlife. It is therefore critical to know if the direct affects of BTK on nontarget Lepidoptera will indirectly have a significant impact on other wildlife.

## LITERATURE CITED

BROOKES, M.H., R.W. STARK, & R.W. CAMPBELL (Eds.). 1978. The Douglas-fir tussock moth: a synthesis. Tech. Bull. 1585. Forest Service. U.S. Department Agriculture, Washington, D.C. 331 p.

BROOKES, R.W. CAMPBELL, J.J. COLBERT, R.G. MITCHELL, & R.W. STARK (Tech. Coor.). 1987. Western spruce budworm. Tech. Bull. 1694. Forest Service. U.S. Department of Agriculture, Washington, D.C. 198 p.

COVELL, C.V., Jr. 1984. A field guide to the moths of eastern North America. Houghton Mifflin Co., Boston. 496 p.

DORNFELD, E.J. 1980. The butterflies of Oregon. Timber Press, Forest Grove, Oregon. 276 p.

EIDT, D.C. 1985. Toxicity of *Bacillus thuringiensis* var. *kurstaki* to aquatic insects. Can. Ent. 117:829-837.

FLEXNER, J.L., B. LIGHTHART, & B.A. CROFT. 1986. The effects of microbial pesticides on non-target, beneficial arthropods. Agric. Ecosyst. and Environ. 16:203-254.

FORSBERG, C.W., M. HENDERSON, E. HENRY, & J.R. ROBERTS. 1976. *Bacillus thuringiensis*: its effects on environmental quality. Proc. Internat. Colloq. Invert. Pathol. 1:410-411.

FRANKLIN, J. F., & C.T. DYRNESS. 1988. Natural vegetation of Oregon and

Washington. Oregon State Univ. Press, Oregon State Univ., Corvallis, OR 452 p.

GRIMBLE, D.G., R.C. BECKWITH, & P.C. HAMMOND. 1993. New lepidoptera records for the Blue Mountains of eastern Oregon. PNW-RP-469. Pac. N.W. Res. Sta., Forest Service, U.S. Department Agriculture, Portland, OR. 6 p.

KRIEG, A., & G.A. LANGENBRUCH. 1981. Susceptibility of arthropod species to *Bacillus thuringiensis*. Appendix 1, pp.837-896 in Burgess, H.D. (Ed.), Microbial control of pests and plant diseases 1970-1980. Academic Press, London.

LAFONTAINE, J.D. 1987. The moths of America North of Mexico. Fasc. 27.2 Noctuoidea: Noctuidae (Part). The Wedge Entomol. Res. Found. 237 p.

McFARLAND, N. 1963. The macroheterocera (Lepidoptera) of a mixed forest in western Oregon. Master's Thesis (Unpublished). Dept. Entomol., Oregon St. Univ., Corvallis. 152 p.

——, 1975. Larval foodplant records for 106 species of North American moths. J. Lepid. Soc. 29:112-125.

McGUGAN, B.M. (Coor.). 1958. Forest lepidoptera of Canada- Recorded by the forest insect survey. Vol.1 (Papilionidae to Arctiidae), Forest Biology Division, Canada Dept. Agric., Ottawa. 76 p.

MILLER, J. C. 1990. Field assessment of the effects of a microbial pest control agent on nontarget Lepidoptera. Amer. Entomol. 36(2):135-139.

——, 1992. Effects of a microbial insecticide, *Bacillus thuringiensis kurstaki*, on nontarget lepidoptera in a spruce budworm-infested forest. J. Res. Lepidoptera 29 (4):267-276.

NIWA, C.G., M.J. STELTZER, & R.C. BECKWITH. 1987. Effects of *Bacillus thuringiensis* on parasites of western spruce budworm (Lepidoptera: Tortricidae). J. Econ. Entomol. 80:750-753.

PARSONS, G.L., G. CASSIS, A.R. MOLDENKE, J.D. LATTIN, N.H. ANDERSON, J.C. MILLER, P. HAMMOND, & T.D. SCHOWALTER. 1991. Invertebrates of the H.J.Andrews Experimental Forest, Western Cascade Range, Oregon. V: An annotated list of insects and other arthropods. PNW-GTR-290. Forest Service. U.S. Department of Agriculture, Washington, D.C. 168 p.

PEACOCK, J.W., & D.F. SCHWEITZER. 1993. Results of Bt (FORAY 48B) bioassays on non-target Lepidoptera. Proc. USDA Interagency Gypsy Moth Res. Forum. USDAFS. NEFES. Gen. Tech Rept. (In press).

PRENTICE, R.M. 1962. Forest lepidoptera of Canada- Recorded by the forest insect survey. Vol. 2 (Nycteolidae, Noctuidae, Notodontidae, Liparidae), Forest Entomol. Pathol. Branch, Canada Dept. Agric., Ottawa. 281 p.

——, 1963. Forest lepidoptera of Canada- Recorded by the forest insect survey. Vol. 3 (Lasiocampidae, Thyatiridae, Drepanidae, Geometridae). Forest Entomol. Pathol. Branch, Canada Dept. Agric., Ottawa. 543 p.

——, 1965. Forest lepidoptera of Canada- Recorded by the forest insect survey. Vol. 4 (Microlepidoptera). Canada Dept. Forestry, Ottawa. 840 p.

ROCKBURNE, E.W., & J.D. LAFONTAINE. 1976. The cutworm moths of Ontario and Quebec. Research Branch, Canada Dept. Agric., Ottawa. 164 p.

TIETZ, H.M. 1972. An index to the described life histories, early stages,and hosts of the macrolepidoptera of the continental United States and Canada. Allyn Mus. Entomol., Sarasota, FL. 1041 p.

Table 1.  Diurnal lepidoptera, collection dates, and partial larval host plants list, collected
from the Blue Mountains, Oregon, 1992.

| Species | No. | Dates[1] | Host plants[2] |
|---------|-----|----------|----------------|
| **ARCTIIDAE** | | | |
| Gonophaela vermiculata (Grote) | 4 | 9.VII | Hrb; BORAGIN., Mertensia sp. |
| **HESPERIIDAE** | | | |
| Erynnis persius (Scudder | 8 | 12.V-8.VI | Shrb; SALIC., Salix sp. |
| Hesperia juba (Scudder) | 11 | 11.V-14.VIII | Grs; PO. |
| Ochlodes sylvanoides (Boisduval) | 19 | 9.VII-11.VIII | Grs; PO. |
| Polites peckius (Kirby) | 5 | 9.VI-14.VII | Grs; PO. |
| Polites sonora (Scudder) | 4 | 8.VI-9.VI | Grs; PO. |
| Pyrgus communis (Grote) | 20 | 12.V-14.VIII | Hrb; MALV. |
| Pyrgus ruralis (Boisduval) | 3 | 19.V-14.VIII | Hrb |
| **LYCAENIDAE** | | | |
| Celastrina argiolus (Linnaeus) | 1 | 12.V | Hdw |
| Everes comyntas (Godart) | 2 | 12.V-13.V | Hrb; FAB. |
| Glaucopsyche lygdamus (Doudleday) | 8 | 12.V-19.V | Hrb; FAB. |
| Icaricia acmon (Westwood & Hewitson) | 3 | 28.V-16.VII | Hrb; POLYGON., Eriogonum sp. |
| Icaricia icarioides (Boisduval) | 14 | 12.V-21.VII | Hrb; FAB., Lupinus sp. |
| Incisalia eryphon (Boisduval) | 6 | 12.V-26.V | Con; PIN., Pinus sp. |
| Lycaeides melissa (Edwards) | 7 | 9.VII-10.VII | Hrb; FAB., Lupinus sp. |
| Lycaena editha (Mead) | 33 | 8.VI-14.VIII | Hrb; POLYGON. |
| Lycaena helloides (Boisduval) | 5 | 26.V-30.VII | Hrb; POLYGON. |
| Lycaena heteronea (Boisduval) | 10 | 8.VI-21.VII | Hrb; POLYGON., Eriogonum sp. |
| Lycaena mariposa (Reakirt) | 41 | 8.VI-21.VII | Shrb; ERIC.,Vaccinium sp. |
| Lycaena nivalis (Boisduval) | 7 | 26.V-10.VII | Hrb; POLYGON., Polygonum sp. |
| Mitoura spinetorum (Hewitson)[a] | 2 | 30.VI-2.VII | Hrb; LORANTH., Arceuthobium sp. |
| Plebejus saepiolus (Boisduval) | 47 | 12.V-28.VII | Hrb; FAB., Trifolium sp. |
| Satyrium sylvinus (Boisduval)[a] | 2 | 10.VII-11.VII | Shrb; SALIC., Salix sp. |
| Strymon melinus (Hubner) | 5 | 26.V-28.VII | Hrb |
| **NYMPHALIDAE** | | | |
| Boloria epithore (Edwards) | 2 | 8.VI | Hrb; VIOL., Viola sp. |
| Chlosyne palla (Boisduval) | 9 | 26.V-28.VII | Hrb; ASTER. |
| Euphydryas chalcedona (Doubleday) | 20 | 18.V-9.VII | Hrb; SCROPHULARI, Penstemon sp. |
| Euphydryas editha (Boisduval) | 2 | 27.VII | Hrb; PLANT |

|  |  |  | AGINACEAE, Plantago sp. |
|---|---|---|---|
| Limenitis lorquini (Boisduval) | 8 | 8.VII-14.VIII | Shrb; SALIC., Salix sp. |
| Nymphalis antiopa (Linnaeus) | 5 | 19.V-11.VIII | Shrb; SALIC., Salix sp. |
| Nymphalis milberti (Godart) | 8 | 19.V-26.V | Hrb; URTIC., Urtica sp. |
| Phyciodes campestris (Behr) | 11 | 27.V-29.VII | Hrb; ASTER., Aster sp. |
| Phyciodes mylitta (Edwards) | 16 | 12.V-5.VIII | Hrb; ASTER. |
| Polygonia faunus (Edwards) | 2 | 12.V-30.VII | Hdw |
| Polygonia satyrus (Edwards) | 11 | 12.V-4.VIII | Hrb; URTIC., Urtica sp. |
| Speyeria atlantis (Edwards) | 4 | 2.VI-19.VI | Hrb; VIOL., Viola sp. |
| Speyeria zerene (Boisduval) | 14 | 8.VI-23.IX | Hrb; VIOL., Viola sp. |
| Speyeria cybele (Fabricius) | 8 | 8.VII- 14.VIII | Hrb; VIOL., Viola sp. |
| Speyeria hydaspe (Boisduval) | 28 | 26.V-14.VIII | Hrb; VIOL., Viola sp. |
| Speyeria mormonia (Boisduval) | 6 | 8.VI-11.VIII | Hrb; VIOL., Viola sp. |
| Vanessa annabella (Field) | 3 | 12.V-9.VI | Hrb; MALV. |
| Vanessa atalanta (Linnaeus) | 4 | 9.VI-16.VIII | Hrb; URTIC., Urtica sp. |
| Vanessa cardui (Linnaeus) | 27 | 12.V-21.VII | Hrb; ASTER., Cirsium sp. |

**PAPILIONIDAE**

| Papilio eurymedon (Lucas) | 2 | 2.VI-8.VI | Shrb; RHAMN., Ceanothus sp. |
|---|---|---|---|
| Papilio zelicaon (Lucas) | 1 | 19.V | Hrb; API. |

**PIERIDAE**

| Anthocaris sara (Lucas) | 9 | 12.V-2.VI | Hrb; BRASSIC. |
|---|---|---|---|
| Colias alexandra (Edwards) | 1 | 9.VII | Hrb; FAB., Astralagus sp. |
| Colias interior (Scudder) | 8 | 8.VI-19.VI | Shrb; ERIC., Vaccinium sp. |
| Neophasia menapia (Felder) | 8 | 27.VII-5.VIII | Con; PIN. |
| Pieris napi (Linnaeus) | 26 | 12.V-6.VIII | Hrb; BRASSIC. |
| Pieris rapae (Linnaeus) | 3 | 12.V-19.V | Hrb; BRASSIC. |

**SATYRIDAE**

| Cercyonis oetus (Boisduval) | 2 | 9.VII-14.VII | Grs; PO. |
|---|---|---|---|
| Cercyonis pegala (Fabricius) | 49 | 8.VII-14.VIII | Grs; PO. |
| Coenonympha tullia (Linnaeus) | 18 | 12.V-14.VIII | Grs; PO. |
| Erebia epipsodea (Butler) | 6 | 18.V-2.VI | Grs; PO. |

---

[1]Collection dates are written as day=arabic numeral, month=Roman numeral (e.g. 19.VIII is 19 August).

[2]Host plant references: Dornfeld 1980; and Parsons et al. 1991. Abbreviations are Con= conifers, Hdw= hardwoods, Hrb= herbs, Grs= grasses, Shrb= shrubs, API.= APIACEAE, ASTER.= ASTERACEAE, BORAGIN.= BORAGINACEAE, BRASSIC.= BRASSICACEAE, ERIC.= ERICACEAE, FAB.= FABACEAE, LORANTH.= LORANTHACEAE, MALV.= MALVACEAE, PIN.= PINACEAE, PLANTAGIN.= PLANTAGINACEAE, PO.= POACEAE, POLYGON.= POLYGONACEAE, RHAMN.= RHAMNACEAE, SALIC.= SALICACEAE, SCROPHULARI.= SCROPHULARIACEAE, URTIC.= URTICACEAE, VIOL.= VIOLACEAE.

[3]Larvae of this species were collected from host plants and reared to the adult stage.

Table 2.  Relative abundance, flight periods, and partial larval host plants list for lepidoptera
taken in ULV blacklight traps in the Blue Mountains, Oregon, 1992.

| Species | No.[1] | Dates[2] | Host plants[3] |
|---|---|---|---|
| **ALUCITIDAE** | | | |
| Alucita hexadactyla Linnaeus | 1 | 3.VI | |
| | | | |
| **ARCTIIDAE** | | | |
| Cycnia oregonensis (Stretch)[7] | 2 | 29.V-12.VIII | Hrb; APOCYN., Apocynum sp. |
| Grammia nevadensis | 1 | 18.VIII | Hrb |
| (Grote & Robinson) | | | |
| Grammia ornata (Packard) | 620 | 13.V-29.VII | Hrb |
| Lophocampa maculata Harris | 168 | 20.V- 15.VII | Hdw |
| Platarctia parthenos (Harris)[4] | 1 | 10.VI | Hdw |
| Spilosoma vagans (Boisduval) | 2205 | 6.V- 8.VII | Hrb |
| Spilosoma virginica (Fabricius) | 19 | 27.V- 22.VII | Hrb/Hdw |
| | | | |
| **GEOMETRIDAE** | | | |
| Anagoga occiduaria (Walker) | 18 | 13.V- 17.VI | Hdw |
| Biston betularia (Guenee) | 26 | 20.V- 24.VI | Hdw |
| Campaea perlata Guenee | 10 | 27.V- 15.VII | Hdw |
| Caripeta aequalaria Grote | 49 | 20.V- 12.VIII | Con; PIN. |
| Ceratodalia gueneata Packard | 16 | 24.VI- 12.VIII | Hrb |
| Chlorosea banksaria Sperry | 9 | 17.VI- 15.VII | Shrb; RHAMN., Ceanothus sp. |
| Cladara limitaria (Walker) | 3 | 6.V | Con; PIN. |
| Cyclophora pendulinaria (Guenee) | 46 | 6.V- 24.VI | Hdw |
| Drepanulatrix carnearia (Hulst) | 13 | 27.V- 24.VI | Shrb; RHAMN., Ceanothus sp. |
| Drepanulatrix foeminaria (Guenee) | 30 | 6.V- 3.VI | Shrb; RHAMN., Ceanothus sp. |
| Drepanulatrix hulstii (Dyar) | 3 | 23.IX | |
| Drepanulatrix quadraria (Grote) | 27 | 27.V- 15.VII | Shrb; RHAMN., Ceanothus sp. |
| Drepanulatrix unicalcararia (Guenee) | 46 | 13.V- 30.IX | Shrb; RHAMN., Ceanothus sp. |
| Dysstroma brunneata (Packard) | 3 | 29.VII- 5.VIII | Shrb; GROSSULARI., Ribes sp. |
| Dysstroma citrata (Linnaeus) | 25 | 10.VI- 15.VII | Hdw |
| Dysstroma formosa (Hulst) | 175 | 8.VII- 30.IX | Shrb; GROSSULARI., Ribes sp. |
| Dysstroma hersiliata (Guenee) | 2 | 22.VII- 29.VII | Shrb; GROSSULARI., Ribes sp. |
| Dysstroma truncata (Hufnagel) | 1 | 13.V | Hdw |
| Elpiste lorquinaria (Guenee) | 4 | 22.VII- 2.IX | Hdw; BETUL., Alnus sp. |
| Ennomos magnaria (Guenee) | 8 | 5.VIII- 30.IX | Hdw |
| Epirrhoe alternata (Mueller) | 11 | 24.VI- 29.VII | Hrb |
| Epirrhoe sperryi (Herbulot) | 1 | 3.VI | |
| Epirrita autumnata (Borkhausen) | 15 | 3.VI | Hdw/Con |
| | | 23.IX- 30.IX | |
| Euchlaena marginaria (Minot) | 139 | 27.V- 29.VII | Hdw |
| Euchlaena johnsonaria (Fitch) | 1 | 24.VI | Hdw |
| Eudrepanulatrix rectifascia (Hulst) | 5 | 10.VI- 24.VI | Shrb; RHAMN., Ceanothus sp. |
| Eulithis destinata (Moschler) | 85 | 24.VI- 23.IX | Shrb; GROSSULARI., Ribes sp. |

| | | |
|---|---|---|
| Eulithis propulsata (Walker) | 10 | 24.VI- 12.VIII Shrb; SALIC., Salix sp. |
| Eulithis xylina (Hulst) | 165 | 1.VII- 2.IX Shrb; SALIC., Salix sp. |
| Euphyia unangulata (Haworth) | 143 | 27.V- 15.VII Hrb |
| Eupithecia agnesata Taylor | 4 | 29.VII- 12.VIII |
| Eupithecia cretaceata (Packard) | 19 | 13.V- 22.VII Hrb |
| Eupithecia misturata (Hulst) | 14 | 10.VI- 29.VII Shrb; RHAMN., Ceanothus sp. |
| Eupithecia multiscripta (Hulst) | 18 | 27.V- 10.VI |
| Eupithecia subcolorata (Hulst) | 132 | 6.V- 1.VII |
| Eustroma semiatrata (Hulst)[7] | 68 | 27.V- 7.X Hrb |
| | 2 | 12.VIII Con; PIN., Pseudotsuga sp. |
| Gabriola dyari Taylor | 13 | 27.V- 17.VI Con; PIN., Pinus sp. |
| Glena nigricaria (Barnes & McDunnough) | 76 | 1.VII- 19.VIII Shrb; ROS. |
| Hesperumia sulphuraria Packard | | |
| Hydria undulata (Linnaeus) | 4 | 3.VI- 24.VI Hdw |
| Hydriomena furcata (Thunberg) | 5 | 22.VII-19.VIII Hdw |
| Hydriomena perfracta Swett | 2 | 13.V- 10.VI Shrb; SALIC., Salix sp. |
| Hydriomena marinata Barnes&McDunnough | 17 | 6.V- 27.V Con; PIN. |
| Iridopsis emasculata (Dyar) | 240 | 27.V- 22.VII Hdw |
| Itame bitactata (Walker)[7] | 33 | 10.VI- 2.IX Shrb;GROSSULARI., Ribes sp. |
| Itame brunneata (Thunberg) | 70 | 24.VI- 19.VIII Shrb; ERIC., Vaccinium sp. |
| Itame quadrilinearia (Packard) | 2 | 5.VIII Hdw |
| Lambdina fiscellaria (Guenee) | 14 | 19.VIII-30.IX Hdw/Con |
| Leptostales rubromarginaria (Packard) | 1 | 12.VIII Hdw |
| Lobophora montanata Packard | 5 | 6.V- 24.VI |
| Melanolophia imitata (Walker) | 211 | 6.V- 27.V Con; PIN. |
| Mesothea incertata (Walker) | 1 | 3.VI Shrb; ERIC., Vaccinium sp. |
| Nacophora mexicanaria (Grote) | 13 | 20.V- 1.VII |
| Nematocampa limbata (Haworth) | 15 | 22.VII- 12.VIII Con; PIN. |
| Nemoria darwiniata (Dyar) | 109 | 3.VI- 19.VIII Shrb; SALIC., Salix sp. |
| Neoterpes tranguliferata (Packard) | 4 | 6.V- 10.VI Shrb;GROSSULARI., Ribes sp. |
| Nepytia phantasmaria (Strecker) | 1 | 23.IX Con; PIN. |
| Nepytia umbrosaria (Packard) | 15 | 22.VII- 19.VIII Con; PIN. |
| Perizoma costiguttata (Hulst)[7] | 19 | 13.V- 12.VIII |
| Perizoma curvilinea (Hulst) | 2 | 13.V |
| Pero mizon Rindge | 121 | 24.VI- 19.VIII Hdw |
| Pero morrisonaria (H. Edwards) | 1 | 10.VI Con |
| Pero occidentalis (Hulst) | 244 | 6.V- 24.VI Con; PIN. |
| Prochoerodes forficaria (Guenee) | 3 | 6.V- 24.VI Hdw |
| Protitame matilda (Dyar) | 13 | 10.VI- 24.VI Shrb; SALIC. |
| Protoboarmia porcelaria (Guenee) | 1 | 12.VIII Hdw/Con |
| Rheumaptera subhastata (Nolcker) | 1 | 20.V Hdw |
| Sabulodes edwardsata (Hulst) | 1 | 29.VII Con; PIN. |
| Scopula ancellata (Hulst)[4] | 59 | 17.VI- 12.VIII |
| Scopula junctaria (Walker) | 517 | 27.V- 5.VIII Hrb; POLYGON. |
| Scopula luteolata (Hulst) | 88 | 20.V- 12.VIII |
| Scopula sideraria (Guenee) | 16 | 20.V- 24.VI Hrb |

| | | | |
|---|---|---|---|
| Selenia alciphearia Walker | 7 | 13.V- 17.VI | Hdw |
| Semiothisa adonis (Barnes & McDunnough)[7] | 15 | 27.V- 19.VIII | Con |
| Semiothisa denticulata (Packard)[7] | 44 | 6.V- 2.IX | Con; PIN., Larix sp. |
| Semiothisa neptaria (Guenee)[7] | 109 | 6.V- 19.VIII | Hdw |
| Semiothisa sexmaculata (Packard)[7] | 45 | 13.V- 2.IX | Con; PIN., Larix sp. |
| Semiothisa signaria (Walker) | 5 | 10.VI- 5.VIII | Con; PIN. |
| Sericosema juturnaria (Guenee) | 17 | 15.VII- 19.VIII | Shrb; RHAMN., Ceanothus sp. |
| Sicya crocearia Packard | 58 | 8.VII- 19.VIII | Hdw |
| Snowia montaneria Neumoegen | 1 | 10.VI | |
| Spargania magnoliata Guenee | 2 | 10.VI | Hrb |
| Stamnodes blackmorei Swett | 4 | 12.VIII- 2.IX | Hrb |
| Stenoporpia dejecta (Hulst) | 12 | 2.IX- 23.IX | Con |
| Synaxis cervinaria (Packard) | 8 | 13.V- 24.VI | Hdw |
| Synaxis jubararia (Hulst) | 33 | 2.IX- 7.X | Hdw |
| Synchlora aerata (Fabricius) | 33 | 10.VI- 23.IX | Hrb |
| Triphosa haesitata (Guenee)[6] | 2 | 15.V- 30.IX | Hdw |
| Venusia duodecemlineata (Packard) | 9 | 6.V- 10.VI | |
| Venusia pearsalli (Dyar) | 2 | 3.VI- 30.IX | Hdw |
| Xanthorhoe defensaria (Guenee)[7] | 233 | 6.V- 30.IX | Hdw |
| Xanthorhoe macdunnoughi Swett | 4 | 17.VI | |
| Zenophleps lignicolorata (Packard) | 42 | 2.IX- 30.IX | |

## HEPIALIDAE

| | | | |
|---|---|---|---|
| Hepialus mathewi H.Edwards | 4 | 2.IX- 23.IX | Hdw/Con roots |

## LASIOCAMPIDAE

| | | | |
|---|---|---|---|
| Malacosoma californicum (Packard) | 2 | 24.VII | Hdw |
| Malacosoma disstria Hubner | 19 | 22.VII- 19.VIII | Hdw |
| Phyllodesma americana (Harris)[7] | 157 | 6.V- 10.VI | Hdw |
| | | 29.VII- 12.VIII | Hdw |
| Tolype distincta French | 67 | 29.VII- 30.IX | Hdw |

## LYMANTRIIDAE

| | | | |
|---|---|---|---|
| Orgyia pseudotsugata (McDunnough) | 1 | 27.VII | Con; PIN. |

## NOCTUIDAE

| | | | |
|---|---|---|---|
| Abagrotis apposita (Grote) | 1 | 12.VIII | |
| Abagrotis baueri McDunnough | 1 | 12.VIII | |
| Abagrotis mirabilis (Grote) | 3 | 19.VIII- 2.IX | Shrb; CUPRESS., Juniperous sp. |
| Abagrotis nefascia (Smith) | 6 | 24.VI- 19.VIII | |
| Abagrotis placida (Grote) | 1 | 19.VIII | |
| Abagrotis scopeops (Dyar) | 4 | 19.VIII- 30.IX | |
| Abagrotis trigona (Smith) | 2 | 29.VII; 12.VIII | Hdw |
| Abagrotis variata (Grote) | 9 | 10.VI- 12.VIII | |

| | | | |
|---|---|---|---|
| Acerra normalis Grote | 4 | 6.V- 20.V | Hdw |
| Achytonix epipaschia (Grote) | 5 | 29.VII- 19.VIII | Con; PIN., Pseudotsuga sp. |
| Acontia flavipennis (Grote) | 1 | 10.VI | Hrb; MALV. |
| Acronicta fragilis Guenee[5] | 3 | 27.V- 10.VI | Hdw |
| Acronicta grisea Walker | 7 | 27.V- 17.VI | Hdw |
| Acronicta hesperida Smith | 44 | 20.V- 22.VII | Hdw |
| Acronicta impressa Walker | 4 | 6.V- 5.VIII | Hdw |
| Acronicta mansueta Smith | 2 | 6.V- 13.V | |
| Agrochola pulchella (Smith)[5] | 1 | 30.IX | Hdw |
| Agrochola purpurea (Grote) | 97 | 23.IX- 7.X | Hdw |
| Agroperina dubitans (Walker) | 116 | 17.VI- 2.IX | Grs; PO. |
| Agroperina lateritia (Hufnagel) | 6 | 1.VII- 12.VIII | |
| Agrotis obliqua (Smith)[5] | 4 | 24.V- 17.VI | Hrb |
| Agrotis vancouverensis Grote | 13 | 20.V- 10.VI | Hrb |
| Agrotis venerabilis Walker | 9 | 2.IX- 23.IX | Hrb |
| Agrotis ipsilon (Hufnagel)[7] | 313 | 6.V; 22.VII-7.X | Hrb |
| Aletia oxygala (Grote) | 62 | 6.V- 29.VII | Grs; PO. |
| Amphipoea keiferi (Benjamin) | 12 | 23.IX- 30.IX | |
| Amphipoea senilis (Smith) | 25 | 2.IX- 30.IX | |
| Amphipyra tragopoginis (Linnaeus) | 2 | 5.VIII- 19.VIII | Hrb |
| Anaplectoides prasina Denis & Schiffermuller[5] | 3 | 24.VI- 15.VII | Hdw |
| Anaplectoides pressus (Grote) | 4 | 17.VI- 8.VII | Hdw |
| Androloma maccullochi (Kirby) | 16 | 13.V- 27.V | Hrb; ONAGR., Epilobium sp. |
| Andropolia theodori (Grote) | 3 | 5.VIII- 2.IX | Hdw |
| Anepia capsularis (Guenee) | 17 | 10.VI- 29.VII | Hrb; CARYOPHYLL. |
| Anomogyna mustelina (Smith) | 8 | 12.VIII- 30.IX | Con; PIN. |
| Anomogyna vernilis (Grote) | 24 | 12.VIII- 30.IX | Con; PIN. |
| Apamea acera (Smith) | 3 | 22.VII | |
| Apamea alia (Guenee) | 4 | 24.VI- 12.VIII | Grs; PO. |
| Apamea amputatrix (Fitch) | 25 | 10.VI- 30.IX | Hrb/Grs; PO. |
| Apamea antennata (Smith) | 38 | 3.VI- 19.VIII | |
| Apamea auranticolor (Grote) | 22 | 24.VI- 22.VII | Hdw |
| Apamea castanea (Grote) | 3 | 29.VII- 5.VIII | Hrb/Grs; PO. |
| Apamea cinefacta (Grote) | 5 | 10.VI- 8.VII | |
| Apamea finitima Guenee | 6 | 6.V- 17.VI | Grs; PO. |
| Apamea occidens (Grote) | 2 | 10.VI- 24.VI | |
| Apharetra pyralis (Smith) | 6 | 19.VIII- 30.IX | |
| Aseptis binotata (Walker) | 3 | 20.V | Hdw |
| Asticta victoria (Grote)[5] | 6 | 8.VII- 22.VII | |
| Autographa ampla (Walker) | 3 | 8.VII- 12.VIII | Hdw |
| Autographa californica (Speyer)[7] | 7 | 13.V- 30.IX | Hrb |
| Autographa metallica (Grote) | 4 | 24.VI- 5.VIII | |
| Autographa pseudogamma (Grote) | 3 | 24.VI- 1.VII | |
| Behrensia conchiformis Grote | 4 | 6.V | Hdw |
| Brachylomia rectifascia (Smith) | 5 | 5.VIII- 19.VIII | Shrb; SALIC., Salix sp. |
| Caenurgina erechtea (Cramer)[7] | 2 | 22.VII- 5.VIII | Hrb |

| | | | |
|---|---|---|---|
| Chersotis juncta (Grote) | 26 | 24.VI- 29.VII | Hrb |
| Chytonix divesta (Grote) | 62 | 12.VIII- 30.IX | Grs; PO. |
| Crassivesica bocha (Morrison) | 69 | 29.VII- 30.IX | Hrb |
| Crymodes devastator (Brace) | 27 | 22.VII- 23.IX | Hrb/Grs; PO. |
| Crymodes longula (Grote) | 2 | 5.VIII- 12.VIII | |
| Cryphia cuerva (Barnes) | 48 | 1.VII- 2.IX | |
| Cucullia intermedia Speyer | 10 | 6.V- 24.VI | Hrb; ASTER. |
| Cucullia postera Guenee | 2 | 17.VI | Hrb; ASTER. |
| Dargida procincta (Grote) | 3 | 5.VIII- 7.X | Hrb/Grs; PO. |
| Diarsia rosaria (Grote) | 156 | 13.V- 8.VII | Grs; PO. |
| Dicestra oregonica (Grote) | 1 | 27.V | |
| Egira curialis (Grote) | 113 | 6.V- 13.V | Hdw |
| Egira perlubens (Grote) | 18 | 6.V- 3.VI | Con; PIN. |
| Egira simplex (Walker) | 68 | 6.V- 20.V | Hdw |
| Epidemas cinerea Smith | 123 | 23.IX- 7.X | |
| Eremobina claudens (Walker) | 11 | 8.VII- 2.IX | |
| Euplexia benesimilis McDunnough[5] | 4 | 29.V- 10.VI | Hdw |
| Eurois astricta Morrison | 656 | 17.VI- 19.VIII | Shrb; SALIC., Salix sp. |
| Eurois occulta (Linnaeus) | 7 | 8.VII- 12.VIII | Hdw |
| Eutricopis nexilis (Morrison) | 1 | 3.VI | Hrb |
| Euxoa aequalis (Harvey) | 8 | 19.VIII- 23.IX | |
| Euxoa albipennis (Grote) | 1 | 7.X | Hrb |
| Euxoa atomaris (Smith) | 2 | 12.VIII- 19.VIII | |
| Euxoa auripennis LaFontaine | 73 | 29.VII- 23.IX | |
| Euxoa auxiliaris (Grote)[7] | 13 | 20.V- 30.IX | Hrb |
| Euxoa basalis (Grote) | 9 | 12.VIII- 2.IX | |
| Euxoa bicollaris (Grote) | 1 | 17.VI | |
| Euxoa brunneigera (Grote) | 7 | 17.VI- 23.IX | |
| Euxoa castanea LaFontaine | 17 | 8.VII- 12.VIII | |
| Euxoa catenula (Grote) | 1 | 23.IX | Hrb |
| Euxoa choris (Harvey) | 2 | 24.VI- 19.VIII | |
| Euxoa comosa (Morrison) | 2 | 5.VIII- 19.VIII | Grs; PO. |
| Euxoa costata (Grote) | 3 | 24.VI- 19.VIII | Hrb |
| Euxoa declarata (Walker) | 20 | 12.VIII- 30.IX | Hrb |
| Euxoa difformis (Smith) | 213 | 2.IX- 7.X | |
| Euxoa divergens (Walker) | 78 | 27.V- 23.IX | Hrb |
| Euxoa henrietta Smith | 1 | 8.VII | Hrb |
| Euxoa hollemani (Grote) | 2 | 23.IX | |
| Euxoa idahoensis (Grote) | 62 | 3.VI- 19.VIII | Hrb |
| Euxoa infausta (Walker) | 13 | 10.VI- 29.VII | Hrb |
| Euxoa infracta (Morrison) | 11 | 5.VIII- 2.IX | Hrb |
| Euxoa intrita (Morrison) | 5 | 12.VIII- 2.IX | Hrb |
| Euxoa messoria (Harris) | 8 | 19.VIII- 2.IX | Hrb |
| Euxoa munis (Grote) | 1075 | 22.VII- 30.IX | Hrb |
| Euxoa obeliscoides (Guenee) | 1 | 23.IX | |
| Euxoa occidentalis Lafontaine & Byers | 13 | 19.VIII- 30.IX | |
| Euxoa olivalis (Grote) | 2 | 29.VII | |

| | | | |
|---|---|---|---|
| Euxoa olivia (Morrison) | 1 | 30.IX | Hrb |
| Euxoa plagigera (Morrison) | 2 | 29.VII | |
| Euxoa punctigera (Walker) | 3 | 19.VIII- 2.IX | Hrb |
| Euxoa ridingsiana (Grote) | 1 | 5.VIII | Hrb |
| Euxoa satiens (Smith) | 4 | 19.VIII- 2.IX | |
| Euxoa satis (Harvey) | 66 | 10.VI- 23.IX | |
| Euxoa septentrionalis (Walker) | 7 | 10.VI- 2.IX | |
| Euxoa simona McDunnough | 1 | 5.VIII | |
| Euxoa terrena (Smith) | 9 | 24.VI- 29.VII | |
| Euxoa tessellata (Harris) | 12 | 3.VI- 19.VIII | Hrb |
| Feltia jaculifera (Guenee) | 2 | 12.VIII- 2.IX | Hrb |
| Fishia evelina (French) | 206 | 2.IX- 7.X | Hdw |
| Fishia yosemitae (Grote) | 14 | 23.IX- 7.X | |
| Graphiphora haruspica (Grote)[5] | 2 | 29.VII | Shrb; SALIC., Salix sp. |
| Heliothis oregonius (H.Edwards) | 1 | 27.V | |
| Heliothis zea (Boddie)[7] | 13 | 23.IX- 30.IX | Hrb |
| Homohadena fifia Dyar | 2 | 8.VII | |
| Homorthodes furfurata (Grote) | 4 | 3.VI- 8.VII | Hdw |
| Hydraecia medialis (Smith) | 307 | 19.VIII- 7.X | Hrb |
| Hypena humuli Harris[7] | 6 | 6.V- 30.IX | Hrb; URTIC., Urtica sp. |
| Hyppa indistincta Smith[5,7] | 3 | 3.VI- 23.IX | Hdw |
| Hyppa xylinoides (Guenee)[7] | 24 | 3.VI- 19.VIII | Hdw |
| Idia americalis (Guenee)[5] | 4 | 29.VII- 12.VIII | Lichens |
| Lacanobia liquida (Grote) | 5 | 10.VI- 29.VII | Hrb |
| Lacanobia lutra (Guenee)[5] | 6 | 27.V- 17.VI | Hdw/Con |
| Lacanobia nevadae (Grote) | 2 | 10.VI | Hdw; BETUL. |
| Lacanobia subjuncta (Grote & Robinson) | 9 | 27.V- 8.VII | Hdw |
| Lacinipolia circumcincta (Smith) | 159 | 12.VIII- 30.IX | |
| Lacinipolia olivacea (Morrison) | 159 | 3.VI- 30.IX | Hrb |
| Lacinipolia pensilis (Grote) | 14 | 5.VIII- 23.IX | Hrb |
| Lacinipolia strigicollis (Wallengren) | 2 | 12.VIII | |
| Lacinipolia vicina (Grote) | 21 | 29.VII- 2.IX | |
| Lasionycta marloffi (Dyar) | 20 | 27.V- 15.VII | |
| Lasionycta perplexa (Smith) | 116 | 3.VI- 12.VIII | |
| Leucania farcta Grote | 223 | 10.VI- 2.IX | Grs; PO. |
| Leucania insueta Guenee | 39 | 27.V- 10.VI | Grs; PO. |
| Litholomia napaea (Morrison) | 3 | 23.IX- 30.IX | Shrb; SALIC., Salix sp. |
| Lithomoia solidaginis (Hubner)[5] | 1 | 30.IX | Hdw |
| Lithophane atara (Smith)[6] | 2 | 30.IX | |
| Lithophane georgii Grote [6] | 4 | 23.IX- 30.IX | Hdw |
| Luperina innota Smith | 2 | 10.VI- 17.VI | |
| Luperina passer (Guenee)[7] | 8 | 3.VI- 5.VIII | Hrb; POLYGON. |
| Mamestra configurata Walker[7] | 2 | 27.V- 12.VIII | Hrb |

| | | | |
|---|---|---|---|
| Melanchra adjuncta (Guenee)[5,7] | 9 | 27.V- 30.IX | Hdw |
| Merolonche ursina Smith | 11 | 6.V- 3.VI | Hrb; FAB., Lupinus sp. |
| Mycterophora longipalpata Hulst[5] | 1 | 12.VIII | Lichens |
| Mycterophora rubricans Barnes & McDunnough | 2 | 8.VII- 12.VIII | |
| Nedra stewarti (Grote)[5,7] | 5 | 6.V- 19.VIII | Hrb; HYPERIC., Hypericum sp. |
| Nephelodes minians Guenee | 8 | 2.IX- 30.IX | Grs; PO. |
| Nycteola cinereana Neumoegen & Dyar | 1 | 6.V | Shrb; SALIC. |
| Oligia illocata (Walker)[5] | 17 | 2.IX- 23.IX | Hdw |
| Oligia indirecta (Grote) | 16 | 1.VII- 12.VIII | Grs; PO. |
| Oligia tonsa (Grote)[7] | 36 | 3.VI- 23.IX | |
| Oncocnemis chorda (Grote) | 2 | 12.VIII- 30.IX | Hdw |
| Oncocnemis figurata (Harvey) | 5 | 24.VI- 8.VII | Shrb; CAPRIFOLI. |
| Oncocnemis phairi McDunnough | 9 | 23.IX- 30.IX | |
| Orthosia hibisci (Guenee) | 25 | 6.V- 13.V | Hdw |
| Orthosia pulchella (Harvey) | 44 | 6.V- 20.V | Hdw |
| Orthosia segregata (Smith)[4] | 27 | 6.V- 13.V | Hdw |
| Panthea portlandia (Grote) | 36 | 6.V- 29.VII | Con; PIN. |
| Papestra cristifera (Walker)[5] | 39 | 6.V- 5.VIII | Hdw/Con |
| Papestra quadrata (Smith)[4] | 27 | 6.V- 10.VI | Hdw/Con |
| Paradiarsia littoralis (Packard)[4] | 8 | 27.V- 10.VI | Hrb |
| Peridroma saucia (Hubner)[7] | 15 | 27.V- 30.IX | Hrb |
| Phobolosia anfracta (H.Edwards) | 1 | 5.VIII | |
| Platyperigea extima (Walker) | 34 | 29.VII- 30.IX | Hrb |
| Platyperigea meralis (Morrison) | 1 | 8.VII | Hrb |
| Platypolia loda (Strecker) | 16 | 23.IX- 30.IX | Hdw |
| Pleromelloida cinerea (Smith) | 67 | 23.IX- 30.IX | Shrb; CAPRIFOLI. |
| Pleromelloida obliquata (Smith) | 11 | 6.V | Shrb; CAPRIFOLI., Symphoricarpos sp. |
| Polia discalis (Grote) | 32 | 24.VI- 22.VII | Shrb; SALIC., Salix sp. |
| Polia purpurissata (Grote) | 464 | 17.VI- 19.VIII | Hdw |
| Protagrotis obscura Barnes & McDunnough | 10 | 17.VI- 8.VII | |
| Protolampra rufipectus (Morrison) | 28 | 5.VIII- 23.IX | Hdw |
| Protoperigea posticata Harvey | 1 | 23.IX | Hdw |
| Protorthodes curtica (Smith) | 10 | 19.VIII- 2.IX | |
| Pseudaletia unipuncta (Haworth)[7] | 24 | 2.IX- 7.X | Grs; PO. |
| Pseudeva palligera (Grote) | 1 | 22.VII | |
| Pseudorthosia variabilis Grote | 42 | 19.VIII- 23.IX | Hrb |
| Pyrrhia exprimens (Walker)[5] | 1 | 8.VII | Hdw |
| Rancora strigata Smith | 1 | 15.VII | |
| Rhyacia quadrangula (Zetterstedt) | 1 | 27.V | |
| Rhynchagrotis exsertistigma[7] (Morrison) | 27 | 27.V- 30.IX | Hrb |
| Rhynchagrotis insularis (Grote) | 6 | 29.VII- 2.IX | |
| Scoliopteryx libatrix (Linnaeus)[6] | 2 | 6.V | Shrb; SALIC., Salix sp. |

| | | |
|---|---|---|
| Sideridis maryx (Guenee)[4] | 3 | 2.VI |
| Sideridis rosea (Harvey) | 3 | 13.V- 10.VI     Hdw |
| Spaelotis havilae (Grote)[7] | 545 | 13.V- 30.IX     Hrb |
| Spodoptera praefica (Grote)[7] | 54 | 29.VII- 30.IX    Hrb |
| Stretchia muricina (Grote) | 35 | 6.V- 27.V      Hdw |
| Synedoida adumbrata (Behr) | 8 | 27.V- 1.VII     Shrb; ERIC., Vaccinum sp. |
| Synedoida hudsonica (Grote & Robinson)[4] | 22 | 10.VI- 24.VI    Hdw |
| Synedoida ochracea (Behr) | 1 | 10.VI |
| Synedoida sabulosa H.Edwards | 6 | 10.VI- 22.VII |
| Syngrapha celsa (H.Edwards) | 1 | 15.VII          Con; PIN. |
| Syngrapha epigaea (Grote)[5] | 6 | 12.VIII- 19.VIII   Shrb; ERIC., Vaccinum sp. |
| Syngrapha orophila Hampson | 11 | 24.VI- 8.VII    Shrb; ERIC., Vaccinum sp. |
| Syngrapha viridisigma (Grote) | 4 | 22.VII- 19.VIII Con; PIN. |
| Tholera americana (Smith) | 4 | 2.IX- 23.IX |
| Trichoplusia ni (Hubner)[7] | 2 | 30.IX- 7.X      Hrb |
| Ufeus satyricus Grote[6] | 2 | 30.IX           Shrb/Hdw; SALIC. |
| Xestia collaris (Grote & Robinson) | 20 | 12.VIII- 23.IX |
| Xestia dolosa Franclemont[7] | 5 | 1.VII- 23.IX     Hrb |
| Xestia oblata (Morrison)[7] | 164 | 27.V- 30.IX     Hdw |
| Xestia smithii (Snellen) | 9 | 24.VI- 2.IX      Hrb |
| Xylena cineritia Grote[6] | 4 | 6.V- 13.V       Hdw |
| Xylena curvimacula (Morrison)[6] | 2 | 6.V             Hdw |
| Xylena thoracica (Putnam-Cramer)[4,6] | 14 | 6.V;            Hdw<br>23.IX- 30.IX |
| Xylotype acadia Barnes & Benjamin[4] | 2 | 30.IX          Con; PINA., Larix sp. |
| Zale duplicata (Bethune)[4] | 7 | 6.V           Con; PINA. |
| Zotheca tranquilla Grote | 10 | 1.VII- 8.VII    Shrb; CAPRIFOLI.,<br>Sambucus sp. |

**NOTODONTIDAE**

| | | |
|---|---|---|
| Gluphisia septentrionis Walker | 1 | 13.V          Shrb; SALIC. |
| Oligocentria pallida (Strecker) | 1 | 24.VI         Hdw |
| Schizura ipomoeae Doubleday | 3 | 1.VII- 22.VII   Hdw |

**OECOPHORIDAE**

| | | |
|---|---|---|
| Agonopterix alstroemeriana (Clemens) | 13 | 12.VIII- 23.IX |
| Ethmia sp. | 4 | 2.IX- 23.IX |

**PLUTELLIDAE**

| | | |
|---|---|---|
| Ypsolopha sp. | 88 | 5.VIII- 30.IX |

**PTEROPHORIDAE**            54    20.V- 5.IX

**PYRALIDAE**

| | | |
|---|---|---|
| Acrobasis tricolorella (Grote) | 35 | 29.VII- 19.VIII Hdw |
| Catoptria oregonica (Grote) | 42 | 5.VIII- 2.IX |

| | | |
|---|---|---|
| Cosipara tricoloralis (Dyar) | 11 | 22.VII- 5.VIII |
| Crambus leachellus (Zincken) | 262 | 12.VIII- 30.IX |
| Crambus pascuellus (Linnaeus) | 58 | 10.VI- 19.VIII |
| Crambus plumbifimbriellus Dyar | 170 | 3.VI- 12.VIII |
| Dioryctria auranticella (Grote) | 129 | 22.VII- 12.VIII Con; PINA., |
| | | Pinus ponderosa cones |
| Dioryctria baumhoferi Heinrich | 94 | 10.VI- 23.IX |
| Euchromius ocelleus (Haworth) | 1 | 5.VIII |
| Eudonia sp. | 4 | 8.VII |
| Evergestis funalis (Grote) | 45 | 8.VII- 2.IX |
| Jocara trahalis (Grote) | 6 | 8.VII- 19.VIII |
| Loxostege sticticalis (Linnaeus) | 1 | 23.IX |
| Mecyna mustelinalis (Packard) | 80 | 10.VI- 2.IX |
| Mimoschinia rufofascialis (Stephens) | 14 | 10.VI- 12.VIII |
| Nomophila nearctia Munroe | 16 | 23.IX- 30.IX |
| Omphalocera occidentalis | 4 | 29.VII- 12.VIII |
| Barnes & Benjamin | | |
| Pediasia dorsipunctella (Kraft) | 81 | 8.VII- 2.IX |
| Pediasia trisecta (Walker) | 21 | 5.VIII- 2.IX |
| Petrophila confusalis (Walker) | 2033 | 10.VI- 19.VIII |
| Pima fulvirugella (Ragonot) | 2 | 27.V- 3.VI |
| Pyla fusca (Haworth) | 734 | 27.V- 23.IX |
| Pyrausta fodinalis (Lederer) | 15 | 10.VI- 19.VIII |
| Pyrausta grotei Munroe | 1 | 8.VII |
| Pyrausta nicalis (Grote) | 7 | 10.VI- 22.VII |
| Pyrausta semirubralis (Packard) | 2 | 10.VI |
| Pyrausta subsequalis (Guenee) | 39 | 6.V- 23.IX |
| Pyrausta unifascialis (Packard) | 31 | 6.V- 10.VI |
| Saucrobotys fumoferalis (Hulst) | 18 | 20.V- 12.VIII |
| Scoparia sp. | 249 | 3.VI- 2.IX |
| Sitochroa chortalis (Grote) | 2 | 3.VI- 24.VI |
| Udea itysalis (Walker) | 54 | 10.VI- 5.VIII |
| Udea profundalis (Packard) | 19 | 3.VI- 8.VII |

## SATURNIIDAE

| | | | |
|---|---|---|---|
| Antheraea polyphemus (Cramer) | 4 | 13.V- 8.VII | Hwd |
| Hyalophora euryalus (Boisduval) | 16 | 6.V- 17.VI | Shrb; RHAMN., Ceanothus sp. |

## SPHINGIDAE

| | | | |
|---|---|---|---|
| Hemaris diffinis (Boisduval) | 2 | 13.V- 20.V | Shrb; CAPRIFOLI., |
| | | | Symphoricarpos sp. |
| Hyles lineata (Fabricius)[7] | 16 | 6.V- 24.VI | Hrb; ONAGR., |
| | | 5.VIII- 19.VIII | Epilobium sp. |
| Paonias myops (J.E.Smith) | 7 | 20.V- 10.VI | Hdw |
| Smerinthus cerisyi Kirby | 86 | 6.V- 12.VIII | Shrb; SALIC., Salix sp. |
| Sphinx drupiferarum (J.E.Smith) | 2 | 10.VI | Shrb; ROS. |

Sphinx vashti Strecker                     232   6.V- 8.VII        Shrb; CAPRIFOLI.,
                                                                   Symphoricarpos sp.

## THYATIRIDAE
Ceranemota tearlei (H.Edwards)9       23.IX- 30.IX
Euthyatira semicircularis (Grote)      2   24.VI
Habrosyne scripta Gosse                2   24.VI              Shrb; ROS., Rubus sp.

## TORTRICIDAE
Acleris brittania Kraft                 81   12.VIII- 30.IX
Archips cerasivorana (Fitch)             2   29.VII- 5.VIII   Hdw
Choristoneura rosaceana (Harris)        38   24.VI- 12.VIII   Hdw
Choristoneura occidentalis Freeman      59   15.VII- 12.VIII  Con; PIN.
Clepsis persicana (Fitch)                8   10.VI- 8.VII     Hdw
Eana argentana (Clemens)               137   10.VI- 5.VIII
Epiblema sp.                             4   10.VI- 24.VI
Eucosma agricolana (Walsingham)          3   3.VI- 10.VI
Hystrichophora stygiana (Dyar)          50   17.VI- 19.VIII
Olethreutes cespitana (Hubner)          26   6.V- 10.VI       Hdw
Olethreutes galaxana Kraft               2   10.VI
Olethreutes glaciana (Moschler)          1   10.VI            Hdw
Pelochrista sp.                        245   10.VI- 19.VIII
Rhyacionia sp.                           4   10.VI- 15.VII    Con; shoot borers

[1]Total number of specimens taken in blacklight traps over trapping period, May 6 through October 7.

[2]Dates are mid-points of weekly trapping periods; written as day=arabic numeral, month= Roman numeral (e.g. 19.VIII is 19 August).

[3]Host plant references: Covell 1984; Lafontaine 1987; McFarland 1963, 1975; McGugan 1958; Parsons et al. 1991; Prentice 1962, 1963, 1965; Rockburne and Lafontaine 1976; Tietz 1972. Abbreviations are: Con= conifers, Hdw= hardwoods, Hrb= herbs, Grs= grasses, Shrb= shrubs, APOCYN.= APOCYNACEAE, ASTER.= ASTERACEAE, BETUL.= BETULACEAE, CAPRIFOLI.= CAPRIFOLIACEAE, CARYOPHYLL.= CARYOPHYLLACEAE, CUPRESS.= CUPRESSACEAE, ERIC.- ERICACEAE, FAB.= FABACEAE, GROSSULARI.= GROSSULARIACEAE, HYPERIC.= HYPERICACEAE, MALV.= MALVACEAE, ONAGR.= ONAGRACEAE, PIN.= PINACEAE, PO.= POACEAE, POLYGON.= POLYGONACEAE, RHAMN.= RHAMNACEAE, ROS.= ROSACEAE, SALIC.= SALICACEAE, URTIC.= URTICACEAE.

[4]New species record for Oregon (Grimble et al. 1993).

[5]Previously known only from the Cascades and Coastal Range in Oregon.

[6]Adults overwinter in this species (Rockburne and Lafontaine 1976).

[7]This species known to have more than one generational emergence period per year.

Table 3. Relative population density of moth species with "rare," "uncommon," "common," or "abundant" populations in the Blue Mountains, based upon light trap sampling, 1992.

| Family | Relative population density Rare (1-5)[1] | Uncommon (6-25) | Common (26 to 200) | Abundant (over 200) | Total |
|---|---|---|---|---|---|
| ALUCITIDAE | 1 | - | - | - | 1 |
| ARCTIIDAE | 3 | 1 | 1 | 2 | 7 |
| GEOMETRIDAE | 33 | 27 | 29 | 4 | 93 |
| HEPIALIDAE | 1 | - | - | - | 1 |
| LASIOCAMPIDAE | 1 | 1 | 2 | 0 | 4 |
| LYMANTRIIDAE | 1 | - | - | - | 1 |
| NOCTUIDAE | 96 | 70 | 37 | 9 | 212 |
| NOTODONTIDAE | 3 | - | - | - | 3 |
| OECOPHORIDAE | 1 | 1 | - | - | 2 |
| PLUTELLIDAE | - | - | 1 | - | 1 |
| PYRALIDAE | 8 | 9 | 12 | 4 | 33 |
| SATURNIIDAE | 1 | 1 | - | - | 2 |
| SPHINGIDAE | 2 | 2 | 1 | 1 | 6 |
| THYATIRIDAE | 2 | 1 | - | - | 3 |
| TORTRICIDAE | 6 | 1 | 6 | 1 | 14 |
| Total: | 159 | 114 | 89 | 21 | 383 |
| Percent: | 41.5 | 29.8 | 23.2 | 5.5 | 100. |

[1]Number of species with 5 or less individuals collected in 8 traps at 4 sites over entire trapping period (May-October 1992).

Table 4. Types of larval food sources utilized by macrolepidoptera in the Blue Mountains of Oregon.

| Food sources[1] | No. species | Percent |
|---|---|---|
| Hardwoods | 134 | 44 |
| Herbs/grasses | 130 | 43 |
| Conifers | 30 | 10 |
| Conifers/hardwoods | 6 | 2 |
| Lichens/dead leaves | 2 | 1 |
| Total: | 302 | 100 |

[1]Based on information provided in: Covell 1984; Dornfeld 1980; Lafontaine 1987; McFarland 1963, 1975; McGugan 1958; Parsons et al. 1991; Prentice 1962, 1963, 1965; Rockburne and Lafontaine 1976; Tietz 1972.

# Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera)

P. J. DeVries
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 01238

I. A. Chacon
Museo Nacional, Apartado 749, San Jose, Costa Rica

and

Debra Murray
Estacion Biologica Jatun Sacha, Casilla 1501-218, Tena, Ecuador

**Abstract.** Over one hundred-eighty observations on the host use and ant association of ninety-eight riodinid butterflies are presented — a substantial addition to our understanding of this distinctly neotropical group. These observations are contrasted to previous work, and discussed with respect to apparent patterns of phytophagy, aphytophagy, caterpillar sociality, and ant association. The majority of riodinid species have unknown life histories, and thus we conclude that much more fieldwork is need before a phylogenetic approach to host use and ant association can be established.

## INTRODUCTION

The fact that there are more species of bats than elephants, more little bats than large ones, more species of insects than mammals, and so on vividly demonstrates one of the best known axioms of biodiversity — there is an inverse relationship between body size and number of species (Hutchinson & MacArthur 1959; May 1978; Van Valen 1973). In other words, the species-number game is not for giants. Add to this that the taxonomy of small-bodied organisms is typically less well known than that of larger ones (Mayr 1969), and it is easy to appreciate how crude our understanding of biodiversity really is. However, the importance of biodiversity lies not simply in numbers but in how organisms live and interact within habitats. Thus another general axiom may be added, namely, that within a particular group the basic natural history of small-bodied species will always be less well known than that of larger ones. For example, among butterflies the host relationships and early stages of the papilionids, pierids and nymphalids are more completely known than are those of the lycaenoid butterflies — the Riodinidae and Lycaenidae. In other words, on average less is known about the lycaenoid butterflies mainly because they are small.

The riodinids are a diverse group of small-bodied butterflies that show an almost entirely neotropical distribution. Starting with Hinton (1951), general reviews of lycaenoid biology have typically treated the riodinid butterflies in passing as peculiar neotropical members of the Lycaenidae

(Cottrell 1984; Ehrlich 1958; Pierce 1987; Vane-Wright 1978). Whatever their relationships eventually prove to be, in the absence of solid data and an overall lycaenoid phylogeny, the fact remains that our perception about the biology and evolution of riodinids has been typically inferred from what we know of lycaenids (DeVries 1991a&c). Recent work with riodinids has increased our understanding of them in two complimentary areas. First, modern systematic studies have lent strong support to the idea that the riodinids are monophyletic (Harvey 1987; see also Martin & Pashley 1992; Robbins 1988). Secondly, experimental and morphological studies have pointed to differences between riodinids and lycaenids with respect to their early stage morphology and the evolution of myrmecophily (e.g., Brevignon 1992; Callaghan 1977, 1982, 1986a&b, 1989; DeVries 1988 a & b, 1991b&c; Harvey 1987; Ross 1964, 1966). Even with the advent of this recent interest in the riodinids, our overall grasp of their early-stage biology can be summarized by a historical quote from Scudder (1887, p. 111) who wrote,

> " ... Our knowledge of the Lemoniinae [Riodinidae] is exceedingly meagre, so that we can here draw no decided conclusions. There is, indeed, no greater desideratum in the study of butterflies than a knowledge of the transformation of the principal genera of this subfamily...."

More than a century since Scudder penned these words we still know less about the life histories of riodinids than of any other major group of butterflies.

For a number of years one of us (PJD) has been preparing a treatment of the Costa Rican riodinid fauna. This project has provided an impetus for the authors to make field observations on the early stages of riodinid butterflies in an array of tropical areas. Given the unparalleled destruction of tropical habitats within the last century and the scarcity of such basic information on riodinids, we feel some urgency in making our observations available to other researchers. Accordingly we here summarize some of our riodinid host records gathered during the last 8 years. We also briefly discuss our observations within the context of the review provided in Harvey's (1987) tribal classification, and highlight some aspects of riodinid biology that we feel may be useful for future studies. A more detailed analysis of these and other observations will appear elsewhere.

## METHODS

The records presented here include cases where field-collected eggs were reared to adults, or where caterpillars of various instar were found in the field and subsequently reared to adults, as well as oviposition records where the female was collected and/or positively identified. The records and information pertinent to them is presented in a telescopic format (Table 1). The complete nomenclature of the butterfly taxa treated in this study is found in Table 2 and follows the higher classification of Harvey (1987). Field observations by DeVries originate from Belize, Costa Rica, Panama, Ecuador, Argentina, Madagascar and Hainan Island, China. Those of Chacon are from Costa Rica only, and those of Murray are

from Jatun Sacha, Ecuador only. Coded abbreviations for the geographic locality of each rearing record are listed in Table 3, and those of the families of hosts are found in Table 4. The identity of symbiotic ant taxa found in association with certain caterpillar taxa are listed in Table 5, and information relevant to these records is found within bold, square brackets [ ] under 'Notes' in Table 1.

Information regarding eggs and caterpillars is placed within parentheses ( ) under 'Notes' in Table 1, and the coded information is as follows:

• eggs — *1* = laid singly, *2* = small clusters of two to six eggs, *3* = clusters from seven to sixty eggs, and *amo* = probable ant mediated oviposition.

• caterpillars — *s* = solitary, *sg* = semi-gregarious (tolerant of other individuals, including other instars), and *g* = gregarious (synchronous in feeding and molting).

As in many other groups of butterflies, riodinid caterpillars typically feed on young leaves or shoots. Unless specified otherwise the abbreviation *lvs* in Table 1 refers to young leaves and *flrs* refers to flowers. Under 'Notes' in Table 1 voucher numbers for Chacon's records are found within brackets { }, the records of Murray are abbreviated DM, and all others are those of DeVries. Voucher material from this study has been deposited in the Museo Nacional de Costa Rica, Museum of Comparative Zoology (Harvard University), and the collections of PJD and DM.

## RESULTS AND DISCUSSION

In all, over 180 original natural history observations for 98 species of riodinid butterflies are presented here, including host associations with 37 plant families and one order of insects (Table 1). Many of these records are new, and others corroborate those published previously. We further provide a substantial number of observations on the identity of the ant taxa that associate with some riodinid caterpillars. Although our observations add considerably to the available body of information on riodinids, within the context of their total species richness the sum total of riodinid host records now known remains small. Nevertheless, highlighting some aspects of host relationships and early stage biology may be useful to future workers. Accordingly we discuss the patterns of host use within the context of a tribal level classification (Harvey 1987), and point to various relationships that relate to clutch size, caterpillar behavior, and aphytophagy. Secondly, we discuss some patterns relevant to understanding those taxa that form symbiotic interactions with ants. Finally, we ask what contribution does the information here make to our understanding of the riodinids as a group, and to our understanding of tropical biodiversity in general.

### New Host Records at the Tribal Level

The first summary of hostplant information aimed specifically at understanding the riodinids at the tribal level was compiled by Harvey (1987). With that work as a reference point we may now add a significant number of new hostplant families to seven riodinid tribes. These are as follows: 1) **Euselasiinae** — (*Euselasia*) Melastomataceae; 2) ***incertae sedis*** — (*Eunogyra*) Araceae; 3) **Riodinini** — (*Ancyluris*) Euphorbiaceae; (*Necyria* and *Lyropteryx*) Vochysiaceae, Gesneriaceae; (*Rhetus*)

Table 1.  Information on riodinid biodiversity

| Genus | Species | Host | Locality | plant part | stage | Notes |
|---|---|---|---|---|---|---|
| *Saribea* | | | | | | |
| | *perroti* | undetermined genus (23) | R | lvs | el | N=3 (1, s) |
| *Abisara* | | | | | | |
| | *echerius* | undetermined genus (23) | H | lvs | e | N=1 (1) |
| *Euselasia* | | | | | | |
| | *rhodogyne* | *Clusia odorata* (7) | B | lvs | lp | N >50 (g) * Zotz |
| | *mystica* | *Psidium* spp (24) | SJ, M | lvs | elp | N=>50 (3, g) |
| | *chrysippe* | *Miconia elata* (21) | CH, L | old lvs | e | N= 1 (3) died as second instars |
| | *nr cafusa* | *Eugenia* sp. (24) | CV | old lvs | lp | N=15 (g) |
| | *eulione* | *Psidium* sp. (24) | GC | lvs | lp | N>100 (g) |
| | | *Psidium guajava* (24) | JS | lvs | elp | N>50 (3, g) DM |
| *Mesosemia* | | | | | | |
| | *asa* | *Psychotria macrophylla* (32) | A | lvs | elp | N=10 (1, s) |
| | *carissima* | *Psychotria luxurians* (32) | PL | lvs | lp | N=5 (s) {91-HNP-147; 92-HNP-176} |
| | *nr. tenebricosa* | undetermined genus (32) | JS | lvs | elp | N=2 (1, s) DM |
| | *nr. ephyne* | undetermined genus (32) | JS | lvs | elp | N=1 (1, s) DM |
| | *telegone* | *Psychotria* sp. (32) | P | lvs | lp | N=2 (s) |
| | | *Aphelandra* sp. (1) | P | lvs | lp | N=1 (s) * Aiello |
| | | *Palicourea guianensis* (32) | C | lvs | el | N=1 (s) |
| | *nr. judicialis* | *Faramea* sp. (32) | JS | lvs | lp | N=1 (s) |
| | | *Faramea eurycarpa* (32) | JS | lvs | elp | N=1 (1, s) DM |
| *Leucochimona* | | | | | | |
| | *lagora* | *Diodia* sp. (32) | L, CH | lvs | elp | N=5 (1, s) |
| | | *Borreria* sp. (32) | PL | lvs | lp | N=1 (s) {92-HNP-70} |
| | | *Coccocypselum herbaceum* (32) | PL | lvs | elp | N= 1 (1, s) {92-HNP-70} |
| | | *Hemidiodia ocimifolia* (32) | PL | lvs | elp | N=7 (1, s) {92-HNP-78; 78.2} |
| | *nr. philemon* | undetermined genus (32) | JS | lvs | elp | N=1 (1, s) DM |
| | *nr. molina* | undetermined genus  (32) | CA | lvs | elp | N=6  (1, s) |
| *Eurybia* | | | | | | |
| | *patrona* | *Calathea inocephala* (20) | CV | flrs | lp | N=6 (1, sg) [3, 10] |
| | *elvina* | *Calathea* spp (20) | L, SJ, | flrs | elp | N>10 (1, s) [3, 17] |
| | | *Calathea* spp (20) | B | flrs | elp | N=3 (1, s) [1, 2, 3, 17] |
| | | *Ischnosiphon pruniosus* (20) | B | flrs | lp | N=2 (s) [9, 17] |

| Genus | Species | Host | Locality | plant part | stage | Notes |
|-------|---------|------|----------|------------|-------|-------|
| | *lycisca* | *Calathea* spp (20) | SJ,L,CH | flrs | elp | N>20 (1,s or sg) [1, 2, 3, 9, 16] |
| | | *Calathea marantifolia* (20) | CV | flrs | elp | N= 4 (1, s) [3, 4, 13] |
| | | *Calathea lutea* (20) | CV | flrs | elp | N= 2 (1, s) [13] |
| | | *Calathea crotalifera* (20) | SV | flrs | elp | N =5 (1, s) [5] |
| | | *Calathea cleistantha* (20) | PL | flrs | elp | N>20 (1, s) [?] {91-HNP-38; 139;140} |
| | | *Calathea latifolia* (20) | B | flrs | elp | N=2 (1, s) [1] |
| | | *Ischnosiphon pruniosus* (20) | CV | flrs | elp | N>20 (1, s) [2, 10] |
| | *sp. unknown* | *Renealmia* sp. (37) | GC | flrs | l | N=4 (s) [6] |
| | *nr nicaeus* | *Calathea* nr *inocephala* (20) | GC | flrs | lp | N=4 (sg) [12] |
| | *nr hyacinthina* | *Renealmia* sp. (37) | JS | flrs | lp | N=1 (2, s) [2, 3] |
| *Napaea* | | | | | | |
| | *eucharilla* | *Ananas comosus* (5) | B | lvs | lp | N=1 (s) |
| | | *Ananas comosus* (5) | CV | lvs | lp | N=1 (s) |
| | | *Achmaea magdalenae* (5)s | B | lv | lp | N=1 (s) |
| | | undetermined genus (5) | PL | lvs | lp | N= 24 (s) {91-HNP-196, 92-HNP-177; 163} |
| | *theages* | *Vriesia* sp. (5) | L | lvs | e | N=1 (1) |
| | | *Scaphyglottis* sp. (27) | Pan | lvs | lp | N=1 (s) *Aiello |
| *Cremna* | | | | | | |
| | *actoris* | *Maxilleria* sp. (27) | JS | lvs | lp | N>10 (1) DM |
| | *thasus* | *Catasetum virdiflavum* (27) | B | lvs | elp | N=5 (1, s) |
| | | *Catasetum virdiflavum* (27) | CH | lvs | e | N=2 (1) |
| | | *Oncidium* sp. (27) | B | lvs | lp | N=4 (s) |
| | | *Brassavola nodosa* (27) | Pan | lvs | lp | N=4 (s) *Aiello |
| | | *Mormodeus igneum* (27) | Pan | lvs | lp | N=1 (s) *Aiello |
| *Eunogyra* | | | | | | |
| | *satyrus* | undetermined (0) | GC | lvs | e | N=2 (1) |
| *Hermathena* | | | | | | |
| | *candidata* | *Vriesia* sp. (5) | CA | flrs | e | N=2 (1) |
| *Ancyluris* | | | | | | |
| | *inca* | *Miconia argentea* (21) | C, L, SV | lvs | elp | N>20 (2, sg) |
| | | *Miconia* sp. (21) | R | lvs | lp | N = 8 (sg) |
| | | *Miconia argentea* (21) | B, G | lvs | lp | N=6 (sg) |
| | | *Miconia elata* (21) | G | lvs | lp | N=5 (sg) |
| | *jurgensenii* | *Hyeronima* sp. (11) | C | lvs | e | N=5 (1) |
| | | *Hyeronima oblonga* (11) | PL | lvs | lp | N=1 (s) {92-HNP-89} |
| | | *Hyeronima* sp. (11) | P | lvs | el | N=3 (1) |

| Genus Species | Host | Locality | plant part | stage | Notes |
|---|---|---|---|---|---|
| *Necyria* | | | | | |
| *beltiana* | *Conostegia xalapensis* (21) | PL | lvs | lp | N=1 (1, s) {92-HNP- 75} |
| | *Vochysia guatemalensis* (36) | PL | lvs | elp | N=11 (1, s) {92-HNP- 72; 74.1; 74.2; 95} |
| | *Drymonia warscewicziana* (14) | PL | lvs | lp | N=1 (s) {92-HNP- 116} |
| *Lyropteryx* | | | | | |
| *lyra* | *Vochysia guatemalensis* (36) | PL | lvs | lp | N=1 (s) {92-HNP-173} |
| *Rhetus* | | | | | |
| *arcius* | *Terminalia catapa* (8) | Pan | lvs | lp | N=1 (s) |
| *Chorinaea* | | | | | |
| *faunus* | *Prionostemma aspera* (15) | B | lvs | lp | N=1 (s) |
| *Ithomeis* | | | | | |
| *eulaema* | *Heisteria* sp. (26) | SV | lvs | e | N=1 (3) |
| *Melanis* | | | | | |
| *pixie* | *Albizzia caribaea* (12) | SJ, SA | lvs | elp | N>100 (3,g) |
| *Themone* | | | | | |
| *pais* | *Quiina* sp. (30) | JS | lvs | e | N=1 (1) DM |
| *Lepricornis* | | | | | |
| *strigosa* | *Heteropteris laurifolia* (18) | B | lvs | lp | N=1 (s) |
| *Metacharis* | | | | | |
| *cuparina* | *Heisteria coccinna* (26) | SV | old lvs | lp | N=1 (s) |
| *Charis* | | | | | |
| *nr. anius* | unknown canopy vine | JS | lvs | elp | N=2 (1, s) DM |
| | *Mikania* sp. (2) | JS | lvs | elp | N=2 (1, s) DM |
| *gynaea* | dead leaves | B, G | dead lvs | el | N=2, (1, s) died as 4th instars |
| *cleonus* | dead leaves | JS | dead lvs | el | N=4 (1, s) died as 2d instars DM |
| *cleonus* | dead leaves | GC | dead lvs | el | N=4, (1, s) died as 2d instars |
| *Caria* | | | | | |
| *rhacotis* | *Celtis iguanae* (34) | SV | lvs | el | N=3 (s) |
| *Chalodeta* | | | | | |
| *chaonitis* | *Miconia longifolia* (21) | L | flrs | lp | N=1 (s) |
| *lypera* | undetermined (28) | JS | lvs | lp | N=2 (sg) DM |
| *Lasaia* | | | | | |
| *agesilaus* | *Albizzia caribaea* (12) | SA | lvs | lp | N=1 (s) |
| *Mesene* | | | | | |
| *phareus* | *Inga* sp. (12) | B | old lvs | lp | N=1 (s) |
| *silaris* | *Rinorea* sp. (35) | P | lvs | e | N=3 (1) |

| Genus Species | Host | Locality | plant part | stage | Notes |
|---|---|---|---|---|---|
| *Mesenopsis* | | | | | |
| *bryaxis* | *Miconia argentea* (21) | B, G, P | lvs | lp | N=4 (s) |
| *Symmachia* | | | | | |
| *tricolor* | *Miconia argentea* (21) | B,G,P | lvs | elp | N=5 (1, s) |
| *rubina* | *Trema micrantha* (34) | L | lvs | lp | N=1 (s) |
| *Helicopis* | | | | | |
| *cupido* | *Monatrichardia* sp. (0) | GC | lvs | lp | N >20 (sg, inside rolled leaf) |
| *Anteros* | | | | | |
| *formosus* | *Miconia impediolaris* (21) | L, CH | lvs | lp | N=5 (s) |
| | *Miconia impediolaris* (21) | G | lvs | lp | N=2 (s) |
| | *Conostegia micrantha* (21) | PL | lvs | lp | N=1 (s) {92-HNP-119} |
| | *Vochysia guatemalensis* (36) | PL | lvs | lp | N=1 (s) {92-HNP-98} |
| *aechus* | *Miconia* sp. (21) | GC, JS | lvs | lp | N=5 (s) |
| *Sarota* | | | | | |
| *gyas* | *epiphylls* (17) | B | epiphylls | lp | N=2 (s) |
| *chrysus* | old leaves with epiphylls | B | epiphylls? | e | N=3 (1) |
| | old leaves with epiphylls | L | epiphylls? | e | N=1 (1) |
| *Argyrogrammana* | | | | | |
| *trochilia* | *Tovomitopsis* sp. (7) | JS | lvs | elp | N=1 (1, s) DM |
| | *Garcinia* sp. (7) | JS | lvs | elp | N=3 (1, s) DM |
| *Emesis* | | | | | |
| *fatima* | *Heisteria* sp. (26) | Cacao | lvs | lp | N=1 (s) {67-HN-89} |
| *lucinda* | *Neea* spp (25) | L, CH | lvs | elp | N>50 (2 or 3, g) |
| | *Neea* sp. (25) | PL | lvs | lp | N=24 (g) {91-HNP-188} |
| *mandana* | *Conceveiba pleiostemona* (11) | PL | lvs | lp | N=1 (s) {92-HNP-101} |
| *lacrines* | *Hyeronima oblonga* (11) | PL | lvs | lp | N=2 (s) {92-HNP-39; 122} |
| | *Casearia arborea* (13) | PL | lvs | lp | N=2 (s) {92-HNP-188; 189} |
| *tenedia* | *Clematis haenkeana* (31) | A | lvs | elp | N=6 (1, s) |
| *Lemonias* | | | | | |
| *zygia* | *Croton* sp. (11) | GC | lvs | elp | N=>10 (2, sg, amo) [21] |
| *Thisbe* | | | | | |
| *irenea* | *Croton billbergianus* (11) | B, G | lvs | elp | N>500 (1, s or sg) [1, 2, 3, 9, 15, 22, 24] |

| Genus | Species | Host | Locality | plant part | stage | Notes |
|-------|---------|------|----------|------------|-------|-------|
| | | *Croton billbergianus* (11) | PL | lvs | lp | N=6 (s) [?] {92-HNP-101} |
| | | *Croton* sp. (11) | ER | lvs | lp | N=2 (s) [3] |
| | | *Croton* spp (11) | L, CH | lvs | lp | N>20 (s or sg) [1, 2, 3, 15, 20] |
| | | *Croton* sp. (11) | C | lvs | lp | N=3 (sg) [8] |
| | | *Croton* sp. (11) | Belize | lvs | lp | N=3 (s) [2, 20] |
| | | *Croton* sp. (11) | GC | lvs | lp | N=4 (s) [2, 22] |
| *Juditha* | lycorias | *Cassia alata* (12) | Cañas | lvs | lp | N=1 (s) [?] |
| | molpe | *Inga pezizifera* (12) | C | lvs | lp | N=5 (s) [27] |
| | | *Inga* spp (12) | B | lvs | lp | N=2 (s) [27] |
| | | *Cassia biflora* (12) | P | lvs | elp | N=8 (1, s, amo) [27] |
| | | *Passiflora vitafolia* (28) | P | lvs | elp | N=4 (1, s, amo) [27] |
| | | *Passiflora adenopoda* (28) | C | lvs | lp | N=2 (s) [27] |
| | | *Doliocarpus* sp. (10) | B | lvs | lp | N=6 (s) [27] |
| | | *Stigmaphyllon* sp. (18) | P | lvs | lp | N>10 (s) [27] |
| | | *Tetracera* sp. (10) | B | lvs | lp | N=2 (s) [27] |
| | | *Cardiospermum* sp. (33) | Bel | lvs | elp | N=3 (1, s, amo) [27] |
| | | *Paullinia bracteosa* (33) | B | lvs | lp | N=2 (s) [27] |
| | | *Serjania mexicana* (33) | B | lvs | lp | N=1 (s) [27] |
| | dorilis | *Ochroma lagapus* (4) | T | mem? | e | N=4 (1 on or near membr-acids) [28] |
| *Synargis* | mycone | *Cassia fruticosa* (12) | L, B | lvs | elp | N=6 (1, s) [2] |
| | | *Pithecellobium* sp. (12) | B | lvs | lp | N=3 (s) [1] |
| | | *Gustavia superba* (16) | P | flrs | lp | N=7 (s) [22] |
| | | *Paullinia fibrigera* (33) | P | lvs | lp | N=1 (s) [1] |
| | | *Heteropteris laurifolia* (18) | B | lvs | lp | N=4 (s) [22] |
| | | *Securidaca diversifolia* (29) | B | lvs | lp | N=2 (s) [1] |
| | | *Phryganocydia corymbosa* (2) | B | lvs | lp | N=2 (s) [1, 18, 20] |
| | | *Pachyptera kere* (2) | B | lvs | lp | N=1 (s) [1] |
| | | *Doliocarpus* sp. (10) | B | lvs | elp | N=6 (1, s) [1] |
| | | *Tetracera* sp. (10) | B | lvs | lp | N=2 (s) [1, 2] |
| | | *Omphalea diandra* (11) | FS | lvs | lp | N=7 (s) [2] |
| | phylleus | *Heisteria cocinna* (26) | B | mem? | el | N=9 (1 on membracids, died as first instars) [27] |

| Genus | Species | Host | Locality | plant part | stage | Notes |
|---|---|---|---|---|---|---|
| | | *Ficus* sp. (22) | P | mem? | e | N=4 (1 on or near membr-acids) [27] |
| | | *Pseudobombax septenatum* (4) | P | mem? | e | N=3 (1 on or near membr-acids) [27] |
| | *gela* | *Inga* sp. (12) | JS | lvs | lp | N=3 (s) [2] |
| | *abaris* | *Acalypha* sp. (11) | JS | lvs | lp | N=1 (s) [2] |
| | | *Bauhinia* sp. (12) | JS | lvs | lp | N=4 (sg)[7] DM |
| *Audre* | | | | | | |
| | *nr aurinia* | unknown | V | unknown | lp | N=7 (sg inside ant nests) [21] |
| | *undetermined sp.* | unknown | V | unknown | lp | N≥40 (sg inside ant nests) [21] |
| *Calospila* | | | | | | |
| | *cilissa* | *Stigmaphyllon* spp (18) | L, C, CH | lvs | elp | N=15 (1, s) [1, 14, 17, 26] |
| | *emylius* | *Stigmaphyllon* sp. (18) | JS | lvs | elp | N=6 (1, s) [2] |
| | | *Stigmophyllon* sp. (18) | JS | lvs | lp | N>10 (s) [17] DM |
| *Adelotypa* | | | | | | |
| | *senta* | *Bauhinia* sp. (12) | JS | lvs | lp | N=6 (sg) [7] DM |
| *Menander* | | | | | | |
| | *menander* | *Marcgravia* sp. (19) | B | lvs | lp | N=2 (s) [17] |
| | | *Sourubea* sp. (19) | GC | lvs | elp | N=6 (1, s) [20] |
| | *laobotas* | *Marcgravia* sp. (19) | C | lvs | e | N=2 (1) |
| | *pretus* | *Marcgravia* sp. (19) | L | lvs | lp | N=2 (s) [17] |
| | | *Sourubea* sp. (19) | PL | lvs | lp | N=8 (s) [?] {92-HNP-97; 100;145} |
| *Setabis* | | | | | | |
| | *lagus* | Scale insects (coc) | PL | scales | elp | N=24 (1, s) [3] {92-HNP-124; 127} |
| *Theope* | | | | | | |
| | *virgilius* | *Omphalea diandra* (11) | F, Pan | lvs | elp | N=7 (1, s, amo) [25] |
| | *eleutho* | *Inga* sp. (12) | C | lvs | lp | N=1 (s) [25] |
| | *nr decorata* | *Cecropia insignis* (6) | L | lvs | lp | N>15 (g) [9, but see text] |
| | *nr thestias* | *Maripa panamensis* (9) | B | lvs | elp | N=9 (1, s, amo) [25] |
| | | *Gustavia superba* (16) | P | flrs | lp | N=3 (s) [25] |
| | *nr matuta* | *Pseudobombax septenatum* (4) | P | lvs | elp | N=6 (2, sg, amo) [27] |

| Genus | Species | Host | Locality | plant part | stage | Notes |
|---|---|---|---|---|---|---|
| *Nymphidium* | | | | | | |
| | mantus | *Maripa panamensis* (9) | B, P | lvs | elp | N>10 (1, s, amo) [25] |
| | | *Inga* sp. (12) | B | lvs | elp | N=2 (1, s, amo) [25] |
| | | *Serjania* sp. (33) | B | lvs | elp | N=1 (1, s, amo) [25] |
| | | *Gustavia superba* (16) | P | flrs | lp | N=3 (s) [25] |
| | haematostictum | *Inga* sp. (12) | B | lvs | elp | N= 6 (1, s ) [17] |
| | cachrus | *Inga* spp (12) | SV | lvs | elp | N=6 (2, sg) [3, 11, 24] |
| | | *Inga* sp. (12) | A | lvs | elp | N=5 (2, sg) [3] |
| | | *Inga* sp. (12) | C | lvs | elp | N= 3 (2, sg) [10] |
| | | *Inga ruiziana* (12) | B | lvs | lp | N = 3 [17] |
| | onaeum | *Inga* sp. (12) | CA | lvs | lp | N=10 (s) [3] |
| | | *Cassia fruticosa* (12) | H | lvs | el | N=2 (1, s) [?] |
| | | *Heteropteris laurifolia* (18) | F | lvs | lp | N=8 (sg) [10] |
| | azanoides | *Inga* spp (12) | L, B | lvs | e | N= 3 (1) [3, 14] |
| | nr ninias | *Inga* sp. (12) | GC | lvs | e | N=1 (2) |
| | baoetia | *Passiflora* sp. (28) | JS | lvs | lp | N=1 (s) [?] DM |
| | nr. derufata | *Inga* sp. (12) | JS | lvs | lp | N=2 (s) [12] DM |
| | nr. lisimon | *Inga* sp. (12) | JS | lvs | lp | N=3 (s) [?] DM |
| | leucosia | *Inga* sp. (12) | JS | lvs | lp | N=7 (sg) [19] DM |
| | | *Gustavia longifolia* (16) | JS | flr bracts | lp | N=5 (sg) [19] DM |
| | ascolia | *Senna* sp (12) | JS | lvs | lp | N=4 (s) [?] DM |
| | caricae | *Inga* sp. (12) | JS | lvs | lp | N=4 (sg) [3] |
| | | *Inga* spp (12) | GC | lvs | elp | N=4 (2, sg) [5, 11] |
| | | *Inga* sp. (12) | JS | lvs | lp | N=5 (sg) [7] DM |

Table 2.    LIst of riodinid taxa treated in this study

**Hamearinae**
**Saribea**
perroti Riley, 1932
**Abisara**
echerius lisa Bennett, 1950
**Euselasiinae**
**Euselasia**
rhodogyne patella Stichel, 1927
mystica (Schaus, 1913)
chrysippe (Bates, 1866)
eulione (Hewitson, 1856)
nr cafusa (Bates, 1866)
**Riodininae**
tribe: ***Mesosemiini***
**Mesosemia**
asa asa Hewitson,1869
carissima Bates, 1866
telegone telegone (Boisduval, 1836)
nr. ephyne (Cramer, 1776)
nr. tenebricosa Hewitson, 1877
nr. judicialis Butler, 1874
**Leucochimona**
lagora (Herrich-Schaffer, 1853)
nr. philemon (Cramer, 1775)
nr. molina  (Godman & Salvin, 1855)
tribe: ***Eurybiini***
**Eurybia**
patrona persona Staudinger, 1875
elvina elvina Stichel, 1910
lycisca Westwood, 1851
nr nicaeus (Fabricius, 1775)
nr hyacinthina Stichel, 1910
tribe: ***incertae sedis***
**Napaea**
eucharilla (Bates, 1867)
theages theages Godman & Salvin, 1878
**Cremna**
thasus subrutillia Stichel, 1910
actoris (Cramer, 1776)
**Eunogyra**
satyrus Westwood, 1851
**Hermathena**
candidata (Hewitson, 1874)

tribe: *Riodinini*

**Ancyluris**
inca inca (Saunders, 1850)
jurgensenii jurgensenii (Saunders, 1850)

**Necyria**
beltiana Hewitson, 1870

**Lyropteryx**
lyra cleadas Druce, 1875

**Rhetus**
arcius castigatus Stichel, 1909

**Chorinaea**
faunus bogota (Saunders, 1858)

**Ithomeis**
eulaema imatatrix (Godman & Salvin, 1878)

**Themone**
pais (Hübner, 1820)

**Melanis**
pixie sanguinea Stichel, 1910

**Lepricornis**
strigosa strigosa (Staudinger,1876)

**Metacharis**
cuparina Bates, 1868

**Charis**
nr anius (Cramer, 1776)
gynaea (Godart, 1824)
cleonus (Stoll, 1782)

**Caria**
rhacotis (Godman & Salvin, 1878)

**Lasaia**
agesilaus (latrielle, 1813)

**Chalodeta**
lypera (Bates, 1868)
chaonitis (Hewitosn, 1866)

tribe: *Symmachiini*

**Mesene**
phareus rubella Bates, 1865
silaris (Godman & Salvin, 1878)

**Mesenopsis**
bryaxis melanochlora Godman & Salvin, 1878

**Symmachia**
tricolor hedemanni (Felder & Felder, 1869)
rubina Bates, 1866

tribe: *Helicopini*

**Helicopis**
cupido (Linnaeus, 1758)

tribe: *Charitini*

**Anteros**

formosus micon Druce, 1875

aechus (Stoll, 1781)

**Sarota**

gyas (Cramer, 1775)

chrysus (Stoll, 1782)

tribe: *Emesini*

**Argyrogrammana**

trochilia (Westwood, 1851)

**Emesis**

fatima nobilata Stichel, 1910

lucinda aurimna (Boisduval, 1870)

mandana (Cramer, 1780)

lacrines Hewitson, 1870

tenedia tenedia Felder & Felder, 1861

tribe: *Lemoniini*

**Lemonias**

zygia egaensis (Butler, 1867)

**Thisbe**

irenea (Stoll, 1870)

lycorias (Hewitson, 1853)

**Juditha**

molpe (Hübner, 1803)

dorilis dorilis (Bates, 1866)

**Synargis**

mycone (Hewitson, 1865)

phylleus praeclara (Bates, 1866)

gela (Hewitson, 1853)

abaris (Cramer, 1776)

**Audre**

nr aurina (Hewitson, 1863)

undetermined species

tribe: *Nymphidiini*

**Calospila**

cilissa (Hewitson, 1863)

emylius (Cramer, 1775)

**Menander**

menander menander (Stoll, 1780)

menander thallus (Stichel, 1910)

laobotas (Hewitson, 1875)

pretus picta (Godman & Salvin, 1886)

**Adelotypa**

senta (Hewitson, 1853)

**Setabis**

lagus jansoni (Butler, 1870)

**Theope**

        virgilius virgilius (Fabricius, 1793)
        eleutho Godman & Salvin, 1897
        nr decorata Godman & Salvin, 1878
        nr thestias (Hewitson, 1860)
        nr matuta Godman & Salvin, 1897

**Nymphidium**

        mantus (Cramer, 1775)
        baoetia Hewitson, 1852
        nr. derufata Lathy, 1932
        nr lisimon (Stoll, 1790)
        haematostictum Godman & Salvin, 1878)
        cachrus ascolides (Boisduval, 1870)
        onaeum Hewitson, 1869
        azanoides occidentalis Callaghan, 1986
        ascolia (Hewitson, 1853)
        leucosia (Hübner, 1806)
        nr ninias (Hewitson, 1865)
        caricae (Linnaeus, 1758)

Table 3. Abbreviations for localities

| Country | Locality |
|---|---|
| **Costa Rica** | A = Las Alturas (Puntarenas) |
| | C = Parque Nacional Corcovado (Puntarenas) |
| | SV = Las Cruces (Puntarenas) |
| | L = La Selva (Heredia) |
| | CH = Chilamate (Heredia) |
| | PL = Plastico (Heredia) |
| | SA = San Antonio de Belen (Heredia) |
| | T = Turrialba (Cartago) |
| | M = Rio Macho de Cartago (Cartago) |
| | SJ = Meseta Central of San Jose (San Jose) |
| | R = Finca EL Rodeo (San Jose) |
| | CA = Cañas  (Guanacaste) |
| | H =  Hacienda Santa Maria (Guanacaste) |
| **Belize** | Bel = Mile 30, Belize City |
| **Panama** | B = Barro Colorado Island |
| | G = Gamboa |
| | P = Pipeline Road |
| | CA = Cerro Azul |
| | Pan = near Panama City |
| | ER = El Real, Darien Province |
| | F = Fort Clayton nr Colon |
| **Ecuador** | JS = Jatun Sacha (Napo) |
| | GC = Garza Cocha (Sucumbios |
| **Argentina** | V = Volcan (Jujuy |
| **Madagascar** | R = Ranamofauna National Park |
| **China** | H = 100 s of Haikou City (Hainan) |

Table 4. Abbreviations of host families for riodinid butterflies.

| code | host family |
|------|-------------|
| 0 | — Araceae |
| 1 | — Acanthaceae |
| 2 | — Asteraceae |
| 3 | — Bignoniaceae |
| 4 | — Bombacaceae |
| 5 | — Bromeliaceae |
| 6 | — Cecropiaceae |
| 7 | — Clusiaceae |
| 8 | — Combretaceae |
| 9 | — Convolvulaceae |
| 10 | — Dilleniaceae |
| 11 | — Euphorbiaceae |
| 12 | — Fabaceae |
| 13 | — Flacourtiaceae |
| 14 | — Gesneriaceae |
| 15 | — Hippocrateaceae |
| 16 | — Lecythidaceae |
| 17 | — Lejuniaceae |
| 18 | — Malpighiaceae |
| 19 | — Marcgraviaceae |
| 20 | — Marantaceae |
| 21 | — Melastomataceae |
| 22 | — Moraceae |
| 23 | — Myrsinaceae |
| 24 | — Myrtaceae |
| 25 | — Nyctaginaceae |
| 26 | — Olacaceae |
| 27 | — Orchidaceae |
| 28 | — Passifloraceae |
| 29 | — Polygalaceae |
| 30 | — Quiinaceae |
| 31 | — Ranunculaceae |
| 32 | — Rubiaceae |
| 33 | — Sapindaceae |
| 34 | — Ulmaceae |
| 35 | — Violaceae |
| 36 | — Vochysiaceae |
| 37 | — Zingiberaceae |
| mem | — Homoptera: Membracidae |
| coc | — Homoptera: Coccidae |

Table 5: Numerical codes of ant taxa found in association with riodinid caterpillars. Codes are found with square brackets in Table 1.

| code | Taxon | subfamily |
|---|---|---|
| ? = | ants not collected | |
| 1 = | *Ectatomma ruidum* | (Ponerinae) |
| 2 = | *Ectatomma tuberculatum* | (Ponerinae) |
| 3 = | *Pheidole* sp. | (Myrmicinae) |
| 4 = | *Pheidole biconstricta* | (Myrmicinae) |
| 5 = | *Pheidole* nr *biconstricta* - no. 1 | (Myrmicinae) |
| 6 = | *Pheidole* nr *biconstricta* - no. 2 | (Myrmicinae) |
| 7 = | *Pheidole* nr *biconstricta* - no. 3 | (Myrmicinae) |
| 8 = | *Solenopsis geminata* | (Myrmicinae) |
| 9 = | *Solenopsis* (Diplorhoptrum grp) sp. | (Myrmicinae) |
| 10 = | *Solenopsis* sp. | (Myrmicinae) |
| 11 = | *Megalomyrmex foreli* | (Myrmicinae) |
| 12 = | *Megalomyrmex* sp. | (Myrmicinae) |
| 13 = | *Wasmannia auropunctata* | (Myrmicinae) |
| 14 = | *Wasmannia* sp. | (Myrmicinae) |
| 15 = | *Aphaenogaster araneoides* | (Myrmicinae) |
| 16 = | *Crematogaster brevispinosa* | (Myrmicinae) |
| 17 = | *Crematogaster* sp. | (Myrmicinae) |
| 18 = | *Cephalotes atratus* | (Myrmicinae) |
| 19 = | *Ochetomyrmex* sp. | (Myrmicinae) |
| 20 = | *Camponotus* sp. | (Formicinae) |
| 21 = | *Camponotus distinguendus* | (Formicinae) |
| 22 = | *Camponotus sericeiventris* | (Formicinae) |
| 23 = | *Dendromyrmex* sp. | (Formicinae) |
| 24 = | *Paratrechina* sp. | (Formicinae) |
| 25 = | *Azteca* sp. | (Dolichoderinae) |
| 26 = | *Tapinoma* sp. | (Dolichoderinae) |
| 27 = | *Dolichoderus bispinosus* | (Dolichoderinae) |
| 28 = | *Dolichoderus validus* | (Dolichoderinae) |

Combretaceae; (*Chorinaea*) Hippocrateaceae; (*Ithomeis* and *Metacharis*) Olacaceae; (*Themone*) Quiinaceae; (*Lepricornis*) Malpighiaceae; (*Chalodeta*) Passifloraceae; 4) **Symmachiini** — (*Mesene*) Fabaceae, Violaceae; (*Mesenopsis* and *Symmachia*) Melastomataceae; (*Symmachia*) Ulmaceae; 5) **Charitini** — (*Anteros*) Melastomataceae, Vochysiaceae; (*Sarota*) Lejuniaceae; 6) **Emesini** —(*Emesis*) Olacaceae, Flacourtiaceae, Ranunculaceae; 6) **Lemoniini** — (*Juditha* and *Synargis*) Dilleniaceae, Sapindaceae, Polygalaceae, Lecythidaceae, Bignoniaceae, and potentially Homoptera; and 7) **Nymphidiini** — (*Theope* and *Nymphidium*)

Euphorbiaceae, Moraceae, Convolvulaceae, Lecythidaceae, Sapindaceae, and Bombacaceae.

The host records reported here (Table 1) agree broadly with the monophagous patterns of host use pointed out by Harvey (1987) for the Mesosemiini, and add further support for polyphagy among members of the Emesini. On the other hand, our observations amplify considerably the host records known from the Riodinini, Symmachiini, and Charitini, and suggest that diet breadth for members of these tribes will eventually include an even greater diversity of host plant families than is currently recognized. Our host records are also completely agree with those noted in Harvey (1987) for the Eurybiini. However, our records amplify the patterns noted for members of the Lemoniini by indicating that some taxa may be a great deal more polyphagous than thought previously, while others seem strictly monophagous. For example, we found that some taxa (e.g., *Juditha molpe* and *Synargis mycone*) may use a suite of plant genera and even families as hosts all at the same site. On the other hand, observations on *Thisbe irenea* indicate that this taxon is monophagous on trees in the genus *Croton* from Belize to Ecuador — most of its geographical range.

## Oviposition Patterns and Caterpillar Behavior

Recent work suggests that caterpillar social behavior derives from factors enhancing survivorship and resource utilization. The benefits accrued by aggregated caterpillars have probably led to oviposition patterns facilitating aggregation and social interactions (Fitzgerald 1993; Costa & Pierce 1994). However, we know almost nothing about the relationship between oviposition patterns, clutch size, and degree of social interaction for most groups of butterflies, especially the riodinids. Three points arise from our records. First, the majority of riodinid taxa have caterpillars that feed as solitary individuals, and it is almost certain that the females of all of these taxa lay single eggs. Second, gregarious caterpillars are found within the Euselasiinae (*Euselasia*), Riodinini (*Melanis*) and Emesini (*Emesis*), and as in other Lepidoptera, appears linked to laying clusters of eggs. Available evidence from *Euselasia* and *Hades* suggests this trait may be widespread among members of the Euselasiinae. In contrast, the trait appears labile within *Emesis*, as this genus includes species with both gregarious and solitary caterpillars. Finally, semi-gregarious caterpillars occur in the Eurybiini, Riodinini, Helicopini, Emesini, Lemoniini and Nymphidiini. This trait may occur in both taxa that lay single eggs (*Eurybia*, *Ancyluris*, *Helicopis*, *Thisbe*) and those that lay several eggs in a loose cluster (*Theope*, *Nymphidium*). In those that lay single eggs, gregariousness suggests a non-cannibalistic tolerance of other individuals when caterpillar densities increase on the host. In *Theope* and *Nymphidium* there is some indication that small egg clusters and semi-gregarious caterpillars are traits that may be widespread within these genera.

## Aphytophagy

The habit of feeding on non-vegetable hosts, termed aphytophagy, is well known within the Lycaenidae (Ackery 1990; Cottrell 1984; Fiedler 1991). Several observations point to the possibility that utilization of non-vegetable hosts may occur in more riodinid genera than suspected previously. First, the only real suggestion of aphytophagy in riodinids derives from an exiguous communication by Urich (in Kaye 1921), who stated that *Setabis lagus* caterpillars were predaceous on homopterous nymphs (*Horiola*) infesting Trinidadian cacao plantations. As this record has gone without verification for over 70 years, it was gratifying to demonstrate that *Setabis lagus* in Costa Rica is carnivorous on scale insects, and thereby provide further impetus for examining other members of the genus for the carnivorous habit. Second, although we were unable to verify the diet of *Audre* nr *aurina* and *Audre* sp. found inside ant nests (details will appear elsewhere, DeVries & Martinez, in prep.), two lines of evidence point to the possibility that their diet may include regurgitations provided by their host ants. At no time in the field or in captivity could we induce *Audre* caterpillars to feed on an array of plant matter, and microscopic examination of the frass of both species determined that it contained no fragments of plant material. Furthermore, despite close observations over several months, we found no evidence that caterpillars fed on ant larvae or pupae. Finally, although decidedly inconclusive, we note that direct oviposition on Homoptera by *Synargis phylleus* and *Juditha dorilas* may indicate a aphytophagous habit in these taxa — an oviposition behavior typically observed in *Setabis lagus* females. On the whole, even the few observations here suggest that future work may reveal aphytophagy as a trait in a variety of riodinid taxa.

## Symbioses with Ants

Available evidence suggests that butterfly myrmecophily evolved within the context of associations involving secretion-harvesting ant taxa, and that caterpillars, secretion-producing Homoptera, and plants bearing extrafloral nectaries share ant symbionts (DeVries 1991a&b). Overall, most myrmecophilous butterfly taxa appear to be facultative with respect to their ant symbionts, but a few taxa have evolved species specific associations (DeVries 1991b; DeVries et al. 1993; Fiedler 1991; Thomas et al. 1989). The observations here (Table 1) both support these general ideas and provide a more accurate picture of the variation found among riodinid-ant symbioses. Depending on the taxon, members of the tribes Nymphidiini and Lemoniini show associations with a variety of common secretion-foraging ant species in the subfamilies Ponerinae, Myrmicinae, Formicinae and Dolichoderinae. In contrast, our records and those published previously (Horvitz et al. 1987) provide no indication that members of the Eurybiini (*Eurybia* only) form associations with ants in the Dolichoderinae. However, in this case sampling error cannot be ruled out, and this should be investigated in greater detail.

## The Interaction between Ant Taxa and Caterpillar Diet

Even the few observations here suggest that eventual understanding of host use patterns by riodinids will require accounting for the interactions between both ants and plants. A number of contrasting examples illustrate this (Table 1). First, the polyphagous species *Synargis mycone* may associate with a variety of ant taxa encompassed by four subfamilies, whereas *Thisbe irenea*, which may associate with members of at least three ant subfamilies, is monophagous on *Croton* throughout its geographical range. Second, the polyphagous species *Juditha molpe* appears to have obligate associations with *Dolichoderus bispinosus* ants in Central America, whereas the polyphagous species *Nymphidium mantus* in Panama shows an apparently obligate relationship with the ant genus *Azteca*. Third, the various *Theope* species noted here appear to show a trend toward monophagy (although many more records are needed), but these butterflies appear to have intimate associations with ants in the Dolichoderinae. The one exception of which we are aware is *T.* nr *decorata*. Although caterpillars of this species fed on a plant inhabited by *Azteca* ants, they were tended entirely by *Solenopsis* ants that had small, open air colonies on the large leaves of the plant. Finally, our field observations indicate that *Lemonias* nr *zygia*, *Juditha molpe*, *Theope virgilius*, *T.* nr *thestias*, *T.* nr *matuta*, and *Nymphidium mantus* all represent cases where the choice of host plant by ovipositing female butterflies is mediated by the presence of particular ant taxa, a trait known from some members of the Lycaenidae (Atsatt 1981; Pierce & Elgar 1985).

## Extrafloral Nectaries and Myrmecophiles

The compilation of host records plus demonstration that caterpillars may benefit from drinking extrafloral nectar provided the basis for the idea that plant taxa bearing extrafloral nectaries are important in the diets of myrmecophilous riodinids (DeVries & Baker 1989; DeVries 1991a). The records presented here also support this pattern (e.g., *Synargis*, *Juditha*, *Nymphidium*), but several cases are of particular interest. First, members of the genus *Eurybia* are known to feed only on flowers of the Marantaceae and Zingiberaceae (Harvey 1987; Horvitz et al. 1987). In the latter group, the inflorescence structure may prevent caterpillars from burrowing into the inflorescence as they do in the Marantaceae. Our field observations showed that caterpillars using Zingiberaceae as hosts position their heads over the extrafloral nectaries located on the outside of the cone-like inflorescence bracts, and they are tended by ants that are also feeding at these nectaries (e.g., Schemske 1980). These observations provide the first direct indication that caterpillars in the Eurybiini also drink extrafloral nectar. Secondly, we have found cases where caterpillars were feeding on plants whose shoots were occupied by Homoptera. In cases where the hostplant did not have extrafloral nectaries (e.g., *Synargis gela*, *S. abaris*, some *Juditha molpe*),

we observed caterpillars drinking honeydew secretions directly from the resident Homoptera. In cases where the plants had both extrafloral nectaries and membracids (e.g., *Lemonias zygia, Synargis gela, S. mycone, Juditha molpe, Theope* nr *matuta,* and *Nymphidium caricae*), we observed caterpillars drinking both extrafloral nectar and Homoptera honeydew. Together these observations further highlight the apparent importance of drinking secretions in the diet of myrmecophilous riodinid caterpillars, in addition to their regular fare of leaf tissue.

## Conclusions and Future Considerations

At the time of their classic paper, Ehrlich & Raven (1964) concluded that there were insufficient records available on lycaenoid butterflies (almost none on riodinids) to provide predictive patterns of their host use. Pierce (1985), and more recently Fiedler (1991) brought together a large and diffuse literature that provides the best available synthesis of host use patterns to date on the Lycaenidae. Their studies further elaborate the complex nature of lycaenid life histories, but suggest that patterns of host use are in fact emerging for the Lycaenidae. At the present time there remain two major hurdles to cross before we can resolve lycaenid host evolution in greater detail: the lack of a phylogeny for the Lycaenidae in which to frame host associations, and the absence of host records for most neotropical taxa.

The hurdles for riodinids are different. In his synthesis of riodinid host records, Harvey (1987) indicated that patterns of host use were evident in a few higher taxa (i.e., Hamaerinae, Eurybiini, and *incertae sedis*), but there were insufficient records available for most groups. Since that time, the number of known host records has increased (Brown 1993; Brevignon 1992; Callaghan 1989; DeVries 1988, 1991a, 1992, and those reported here). Considering all available records together indicates that riodinid life histories display a diversity of traits including monophagy and polyphagy, caterpillar growth benefits gained by drinking secretions, caterpillar-ant associations ranging from facultative to obligate species specific, and possibly a modicum of aphytophagy. These traits parallel those known from within the Lycaenidae (Cottrell 1984; Fiedler 1991; Pierce 1987). However, even with the inclusion of this new information and the framework of a higher classification to interpret patterns of host use, our understanding of riodinid host use is conjectural — the host records for at least three quarters of the riodinid species are unknown.

An important aspect to the study of myrmecophilous riodinids concerns identification of ant symbionts. However, most studies of myrmecophilous butterflies (including the present one) are guilty of listing ant symbionts without complete identifications. In part this reflects the small number of qualified ant taxonomists in the world, and the negligence of many butterfly biologists in making proper collections of ants. The positive identification to species in some ant groups (e.g., *Pheidole, Solenopsis, Aphaenogaster, Camponotus,* and *Azteca,* among others) is

difficult or impossible without specimens of the reproductive castes (S. Cover, pers. comm.). Nevertheless, understanding the phylogenetic and ecological patterns of why some riodinid taxa form symbioses with only a particular subgroup within a genus or even with a particular species of ant (e.g., *Juditha molpe*), while others are apparently ant generalists (e.g., *Synargis mycone*) will depend upon correct identification of their ant symbionts. Thus, we urge future workers to take special care to collect strong series of ant symbionts when rearing myrmecophilous species, and to have them properly identified.

As we stressed previously, biodiversity is a suite of different organisms and their often complex interactions within habitats. Why our understanding of riodinid biodiversity is so poor is likely the result of many interacting factors. Such factors may include their small size, their almost exclusive occurrence in neotropical forest habitats, fundamental characteristics of their biology and interactions with other organisms that make them difficult to observe, or combinations of these and other factors. Whatever the ultimate reasons may be, it seems to us that Scudder's (1887) counsel regarding the importance of knowing more about the early stages of the riodinids has lost none of its resonance a century later. To fortify our grasp of riodinid evolution and biodiversity many more rearing records from virtually all of the neotropical subfamilies and tribes are required.

Despite the media's apparent concern over the world-wide devastation of biodiversity, we presently live in a time when grant giving and receiving institutions of science seem concerned almost exclusively with the technology of molecular biology and other types of so called 'big science.' Because technology is often equated with science, this trend will continue to reduce interest in whole-organism biology and natural history in both institutions of higher learning and in the students they produce (e.g., see Erzinclioglu 1993). However, without data from the real world, no matter how sophisticated laboratory techniques or models become, in the absence of natural history they are unlikely to broaden our understanding of the myriad interactions among organisms. The message is simple: future insights into tropical biodiversity in general, and riodinid early stage biology specifically will demand a great deal more field work. It is our hope that this paper will encourage more people to study riodinids than have done so in the past century. One thing is inescapable — technology will not stem the destruction of tropical habitats nor will wishful rhetoric save those riodinid taxa and their interactions with other organisms that will be extirpated during the next hundred years. Now is the time for deeds, not words.

## LITERATURE CITED

ACKERY, P. R. 1990. Biocontrol potential of African lycaenid butterflies entomophagous on Homoptera. J. African Zool. 104: 581-591.

ATSATT, P. R. 1981. Ant dependent food selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). Oecologia 48: 60-63.

BREVIGNON, C. 1992. Elevage de deux Riodininae guyanais *Napaea beltiana* Bates et *Cremna thasus* Stoll. Alexanor 17: 403-4134.

BROWN, K.S. JR. 1993. Neotropical Lycaenidae: an overview. In T. R. New (ed.) Conservation biology of Lycaenidae (butterflies). pp. 45-61. ICUN, Gland, Switzerland.

CALLAGHAN, C. J. 1977. Studies on Restinga butterflies I. Life cycle and immature biology of *Menander felsina* (Riodinidae), a myrmecophilous metalmark. J. Lep. Soc. 20: 36-42.

——. 1982. Notes on immature biology of two myrmecophilous Lycaenidae: *Juditha molpe* (Riodininae) and *Panthiades bitias* (Lycaeninae). J. Res. Lep. 20: 36-46.

——. 1986a. Notes of the biology of *Stalachtis susanna* (Lycaenidae: Riodininae) with a discussion of riodinine larval strategies. J. Res. Lep. 24: 258-263.

——. 1986b. Studies on Restinga butterflies: the biology of *Synargis brennus* (Stichel) (Riodinidae). J. Lep. Soc. 40: 93-96.

——. 1989. Notes on the biology of three riodinine species: *Nymphidium lisimon attenuatum*, *Phaenochitonia sagaris satinus*, and *Metacharis ptolomaeus* (Lycaenidae: Riodininae). J. Res. Lep. 27: 109-114.

COSTA, J. T. & N. E. PIERCE 1994. Social evolution in the Lepidoptera: ecological context and the role of signal enhancement. in J. C. Choe and B. J. Crespi (eds.) Social competition and cooperation in insects and arachnids: vol. 2, evolution of sociality. Princeton University Press, Princeton, New Jersey. (in press)

COTTRELL, C.B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zool. J. Linn. Soc. 80: 1-57.

DeVries, P.J. 1988a. The use of epiphylls as larval hostplants by the neotropical riodinid butterfly *Sarota gyas*. J. Nat. Hist. 22: 1447-1450.

——. 1988b. The larval organs of *Thisbe irenea* (Riodinidae) and their effects upon attending ants. Zool. J. Linn. Soc. 94: 379-393.

——. 1991a. Ecological and evolutionary patterns in riodinid butterflies. *In* Ant-Plant Interactions, C. Huxley and D. F. Cutler (eds.) p. 142-156 Oxford Univ. Press, Oxford

——. 1991b. The mutualism between *Thisbe irenea* and ants, and the role of ant ecology in the evolution of larval-ant associations. Biol. J. Linn. Soc 43: 179-195.

——. 1991c. Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. American Mus. Nov. 3025: 1-23.

DeVries, P. J., J. A. Thomas & R. Cocroft. 1993. A comparison of acoustical signals between *Maculinea* butterfly caterpillars and their obligate host ant species. *Biol. J. Linn. Soc.* 49: 229-238.

DeVries, P.J. & Baker, I. 1989. Butterfly exploitation of a plant-ant mutualism: adding insult to herbivory. J. N.Y. Ent. Soc. 97: 332-340.

Ehrlich, P. R. 1958. The comparative morphology, phylogeny, and higher classification of the butterflies (Lepidoptera: Papilionoidea). Univ. Kansas Sci. Bull. 39: 305-370.

Ehrlich, P. R. & Raven, P. 1965. Butterflies and plants: a study in coevolution. Evol. 18: 596-604.

Enzinclioglu, Y. Z. 1993. On the failure of the natural history museum. J. Nat. Hist. 27: 989-992.

Fiedler, K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner Zoologische Monographien 31: 1-210.

Fitzgerald, T.D. 1993. Sociality in caterpillars. pp. 372-403 in N.E. Stamp and T. E. Casey (eds.) Caterpillars. Routledge, Chapman and Hall, Inc., New York.

Harvey, D. J. 1987. The higher classification of the Riodinidae (Lepidoptera). Ph. D. thesis, University of Texas, Austin, Tx.

Hinton, H.E. 1951. Myrmecophilous Lycaenidae and other Lepidoptera- a summary. Proc. Trans. S. Lond. Entom. and Nat. Hist. Soc. 1949-1950: 111-175.

Horvitz, C.C., Turnbull, C. & Harvey, D. J. 1987. Biology of immature *Eurybia elvina* (Lepidoptera: Riodinidae), a myrmecophilous metalmark butterfly. Ann. Ent. Soc. Am. 80: 513-519.

Hutchinson, G. E. & R. H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. Am. Nat. 93: 117-125.

Kaye, W. J. 1921. A Catalogue of the Trinidad Lepidoptera Rhopalocera (Butterflies) Government Printing office, Trinidad, B.W.I.

Martin, J. A. & Pashley, D. P. 1992. Molecular systematic analysis of butterfly family and some subfamily relationships (Lepidoptera: Papilionoidea). Annals Ent. Soc. Amer. 85: 127-139.

May, R. M. 1978. The dynamics and diversity of insect faunas. Symp. Royal Ent Soc 9: 188-204.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill, New York, N.Y.

Pierce, N. E. 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein rich food plants. Am. Nat. 125: 888-895.

——. 1987. The evolution and biogeography of associations between lycaenid butterflies and ants. Oxford Sur. Evol. Biol. 4: 89-116.

PIERCE, N. E. & ELGAR, M. A. 1985. The influence of ants on host selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behav. Ecol. Sociobiol. 16: 209-222.

ROBBINS, R. K. 1988. Comparative morphology of the butterfly foreleg coxa and trochanter (Lepidoptera) and its systematic implications. Proc. Ent. Soc. Washington 90: 133-154.

ROSS, G. N. 1964. Life history on Mexican butterflies III. The early stages of *Anatole rossi*, a new myrmecophilous metalmark. J. Res. Lep. 3: 81-94.

——. 1966. Life history studies of a Mexican butterfly. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark. Ann. ent. Soc. Amer. 59: 985-1004.

SCHEMSKE, D. W. 1980. The evolutionary siginficance of extrafloral nectar production by *Costus woodsonii* (Zingiberaceae): an experimental analysis of ant protection. J. Animal Ecol. 68: 959-967.

SCUDDER, S. H. 1887. Note on the group Eumaeidi. In Godman, F. D. and O. Salvin 1879-1901 (eds.) pp.110-112. Biologia Centrali Americana. Insecta, Lepidoptera, Rhopalocera. Vol. II, London.

THOMAS J.A., G. W. ELMES, J.C. WARDLAW, & M. WOYCIECHOWSKI. 1989. Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. Oecologia 79: 452-457.

VAN VALEN, L. 1973. Body size and numbers of plants and animals. Evolution 27: 27-35.

VANE-WRIGHT, R.I. 1978. Ecological and behavioural origins of diversity in butterflies. Symp. Roy. Ent. Soc. Lond. 9: 56-70.

# The effect of different foodplants on cocoon crop performance in the Indian tasar silkworm *Antheraea mylitta* Drury (Lepidoptera: Saturniidae)

A.K. Dash[1], B.K. Nayak[2], and M. C. Dash[2]

**Abstract.** Cocoon crop performance through seasonal rearings of *Antheraea Mylitta* Drury larva on three primary foodplants Asan (*Terminalia tomentosa* W. & A.), Arjun (*Terminalia arjuna* W. & A.), Sal (*Shorea robusta* Gaertn.) and three secondary foodplants, Ber (*Ziziphus jujuba* Gaertn.), Sidha (*Lagerstroemia parviflora* Roxb.) and Dha (*Anoegeissus latifolia* Wall.) indicate better performance in winter crops than those of a rainy and autumn season. Sal, among primary foodplants, appeared uneconomical in terms of total cocoon shell (raw silk) production in spite of a superior cocoon formation Overall performance was superior in Asan than all other foodplants during all the seasons. Performance on Ber was higher than Sal and other secondary foodplants, a situation not heretofore documented. The gradation of foodplant with regard to performance (total raw silk production) was, in decreasing order of productivity: Asan, Arjun, Ber, Sal, Sidha, Dha.

## INTRODUCTION

*Antheraea mylitta* Drury is a semidomesticated Indian tasar silkworm exploited commercially for production of tasar silk. At lower altitudes (50-30m ASL), it is trivoltine, reared three times a year in July-August (Rainy cocoon crop), September-October (Autumn cocoon crop) and November-December (Winter cocoon crop). The silkworm is polyphagous feeding on a number of foodplants, of which Asan (*Terminalia tomentosa* W. & A.), Arjun (*Terminalia arjuna* W. & A.) and Sal (*Shorea robusta* Gaertn.) are considered primary and the remainder secondary foodplants (Jolly, 1966; Jolly *et al*, 1974). Evaluation of these foodplants with respect to seasonal cocoon crop productivity has not been made. This paper evaluates tasar silk production by *A. mylitta* fed on six foodplants.

## MATERIAL AND METHODS

At the State Tasar Research Farm (Area 20 ha) Durgapur, Orissa, a number of foodplants were selected at random for rearing of *A. mylitta* larva. The three Combretaceae foodplants chosen were Asan (*T. tomentosa*), Arjun (*T. arjuna*), and Dha (*Anoegeissus latifolia* Wall.). One foodplant from the Dipterocarpaceae, Sal (*S. robusta*) was selected as well as one Melostomaceae, Ber (*Ziziphus jujuba* Gaertn.), and one Lythraceae, Sidha (*Lagerstroemia parviflora* Roxb.). For each foodplant species, 10000 freshly hatched healthy hatchlings were separated into five groups of equal size and brushed onto a number of plants for each of three seasons. The cocoon crop performance was evaluated by effective rate of rearing

---

[1] Department of Zoology, Dr. Jadunath College, Salt Road, Rasalpur, Balasore-756021, Orissa, India.
[2] School of Life Sciences, Sambalpur University, Burla, Orissa.

(ERR% = 100 × total cocoons yielded / total larvae brushed), cocoon weight, pupa weight, and shell weight. These parameters were evaluated for each category of food plant in different rearing seasons by standard laboratory techniques. The data were statistically analyzed following Sokal & Rohlf (1969). The experiment was repeated yearly from 1985 to 1989 for all three rearing seasons.

## RESULTS

Table 1 presents data on cocoon crop performances on six foodplants. Crop performance as weight of cocoon, pupa and shell on all foodplants was uniformly highest in winter, followed by autumn, with rainy season last, except Sal reared autumn pupa that had the lowest weight. The ERR% on different foodplants was highest in winter and lowest in autumn, except Sal. The maximum ERR% was during rainy and minimum in winter crops).

Table 1. Cocoon crop performance in rearing of *A. mylitta* on different foodplants during Rainy (R), Autumn (A) and Winter (W) seasons (Mean ± Standard Deviation).

| Food Plants | Rearing Season | ERR (%) | Cocoon weight (gm) | Pupa weight (gm) | Shell weight (gm) |
|---|---|---|---|---|---|
| Asan | R | 34.05 ± 0.32 | 10.85 ± 0.23 | 9.72 ± 0.21 | 1.13 ± 0.03 |
| (*T. tomentosa*) | A | 26.52 ± 1.11 | 12.84 ± 0.30 | 11.40 ± 0.30 | 1.44 ± 0.03 |
| | W | 46.11 ± 1.85 | 14.35 ± 0.19 | 12.59 ± 0.48 | 1.96 ± 0.02 |
| Arjun | R | 15.45 ± 1.58 | 12.38 ± 0.35 | 10.93 ± 0.33 | 1.44 ± 0.03 |
| (*T. arjuna*) | A | 23.02 ± 1.10 | 11.46 ± 0.36 | 10.24 ± 0.37 | 1.22 ± 0.12 |
| | W | 42.21 ± 0.72 | 13.54 ± 0.31 | 11.95 ± 0.35 | 1.58 ± 0.08 |
| Sal | R | 15.45 ± 1.58 | 12.38 ± 0.35 | 10.93 ± 0.33 | 1.44 ± 0.03 |
| (*S. Robusta*) | A | 9.43 ± 0.70 | 12.46 ± 0.25 | 10.84 ± 0.60 | 1.62 ± 0.05 |
| | W | 7.52 ± 0.51 | 13.72 ± 0.25 | 11.92 ± 0.26 | 1.79 ± 0.02 |
| Ber | R | 23.01 ± 1.34 | 9.83 ± 0.37 | 8.87 ± 0.37 | 0.95 ± 0.01 |
| (*Z. jujuba*) | A | 18.18 ± 1.62 | 11.36 ± 0.21 | 0.22 ± 0.49 | 1.14 ± 0.01 |
| | W | 26.66 ± 1.48 | 13.26 ± 0.33 | 11.83 ± 0.31 | 1.43 ± 0.02 |
| Sidha | R | 10.59 ± 1.25 | 8.91 ± 0.52 | 8.08 ± 0.51 | 0.84 ± 0.01 |
| (*L. parviflora*) | A | 6.38 ± 1.08 | 9.75 ± 0.25 | 8.81 ± 0.25 | 0.94 ± 0.01 |
| | W | 13.07 ± 1.65 | 12.19 ± 0.15 | 11.00 ± 0.13 | 1.19 ± 0.03 |
| Dha | R | 5.66 ± 1.24 | 8.69 ± 0.38 | 7.95 ± 0.38 | 0.74 ± 0.01 |
| (*A. latifolia*) | A | 3.58 ± 0.45 | 9.13 ± 0.32 | 8.31 ± 0.32 | 0.81 ± 0.01 |
| | W | 8.44 ± 1.51 | 9.41 ± 0.39 | 8.55 ± 0.39 | 0.86 ± 0.01 |

Table 2.    Some ecological parameters (Mean ± Standard Deviation) during
            rearing period of *A. mylitta*

| Rearing Season | Temperature (°C) | Relative Humidity (%) | Rainfall (mm) | Stormy Weather Period (hrs.) |
|---|---|---|---|---|
| Rainy (July-Aug.) | 31.85 ± 0.75 | 83.04 ± 2.22 | 231.29 ± 5.38 | 4.48 ± 1.82 |
| Autumn (Sept.-Oct.) | 28.67 ± 1.02 | 76.51 ± 1.79 | 88.97 ± 3.10 | 9.82 ± 3.15 |
| Winter (Nov.-Dec.) | 20.27 ± 1.04 | 65.39 ± 1.39 | 19.44 ± 2.04 | 0.41 ± 0.12 |

Table 3.   Total cocoon shell (raw silk in gm) production based on effective rate of
           rearing (ERR × shell weight) of *A. mylitta* in different foodplant and seasons

| Rearing Season | Food Plants | | | | | |
|---|---|---|---|---|---|---|
| | Asan | Arjun | Sal | Ber | Sidha | Dha |
| Rainy | 38.48 | 31.70 | 22.25 | 21.86 | 8.90 | 4.19 |
| Autumn | 38.19 | 28.08 | 15.28 | 20.69 | 6.00 | 2.90 |
| Winter | 90.38 | 66.69 | 13.46 | 38.12 | 15.55 | 7.26 |

The ANOVA test on seasonal variation of all cocoon crop parameters in individual foodplants indicated significant ($P < 0.05$) differences except Dha-reared pupa weight. The t-test also indicated significant ($p < 0.05$) seasonal differences of all above crop parameters in different foodplants except Sal-reared rainy autumn cocoon weight, pupa weight and Dha-reared rainy-autumn, winter-autumn cocoon weight and winter-autumn and rainy-autumn pupa weight.

In winter Asan produced a superior crop compared with other foodplants in all parameters (Table 1). Asan reared larvae showed a significantly higher value in ERR% in all seasons, in cocoon and pupa weight during autumn and winter crop and in shell weight during the winter crop. Sal reared *A. mylitta* exhibited highest cocoon and pupa weight in rainy crop and highest shell weight in both rainy and autumn crop (Table 1). However, the total quantity of cocoon shell (raw silk) production, based on average ERR% values (ERR% × shell weight), Sal rearing was inferior to Asan and Arjun rearing in the rainy season, Asan, Arjun and Ber rearing in autumn season, and Asan, Arjun, Ber, and Sidha rearing in winter season (Table 3). Thus considering cocoon shell production in different seasons, Asan ranks first followed by Arjun and Ber (Table 3). The superiority of Sal was reflected only in production of tough, heavier cocoons, which in terms of ERR% rendered uneconomical cocoons due to poor silk productivity. Performance on so-called secondary foodplants like Ber and Sidha was higher in comparison to Sal.

The ANOVA test on foodplant variation of all cocoon crop parameters in a particular rearing season indicated significant ($p < 0.01$) difference.

The t-test also indicated significant (p < 0.05) foodplant differences among all cocoon crop parameters in any given season except the winter ERR% on Sal-Dha, autumn cocoon weight grown on Arjun-Ber and Asan-Sal, Winter cocoon weight on Arjun-Sal and Arjun-Ber, rainy cocoon weight on Sidha-Dha, winter pupa weight on Arjun-Sal, Arjun-Ber, Sal-Ber, rainy pupa weight on Sidha-Dha and autumn shell weight on Arjun-Ber.

There was significant interaction between different foodplant and seasonal changes for each cocoon crop parameter. It was evident from the results that winter season crops were more stable and showed higher shell productivity during trivoltine tasar silkworm rearing. Cocoon crop performances on Sal was not more profitable than Asan, Arjun and Ber due to poorer yield of raw silk. Hence the ranking of foodplant in terms of decreasing silk productivity was in the order of Asan, Arjun, Ber, Sal, Sidha, Dha.

## DISCUSSION

The superiority of the winter cocoon crop to other seasonal crops, regardless of foodplant, might be due to prevalent lower average temperature (20°C), humidity (6%) and drier atmosphere (lowest rainfall of 19 mm) which facilitates increased spinning of cocoons (Table 2). Yokoyama (1962) reported that *Bombyx mori* yields superior quality cocoons at optimum temperatures (22-23°C) and humidity (60-70%). Krishnaswami *et al.* (1973) stressed the requirement of an optimum environment for maximum productivity of good quality cocoons and comparatively drier atmosphere (60-70% RH) during spinning for better cocoon yield with *B. mori* . Sengupta (1986) remarked that larger ERR% of *A. mylitta* in winter season is due to climatic limitations.

The lowest cocoon quality during the rainy season might be due to high temperatures (31°C), RH (83%) and rainfall (231 mm) (Table 2). Ullal and Narasimhanna (1987) reported that high temperature followed by strong fluctuation results in poor quality cocoons of *B. mori*. Tanaka (1964) remarked that the rainy season is unsuitable for rearing of *B. mori* due to high RH and changing temperature. Sarkar (1980) and Anonymous (1984) stated that sudden variation in temperature is harmful to rearing *Philosamia ricini* larvae. Krishnaswami *et al.* (1973) reported that temperature and RH exceeding 20-26°C and 60-70% respectively affects cocoon quality of *B. mori*. Jolly *et al.* (1974) remarked that heavy rainfall disrupts spinning of *A. mylitta* resulting in inferior cocoons.

Although the autumn cocoon crop ranked second in quality to the winter crop, the cause of its lower ERR% compared with the rainy crop might be due to occurrence of longer stormy weather durations (9.82 hours as against 4.48 hours) during this season causing high larval mortality (Table 2). Krishnaswami *et al.* (1973) remarked about poor silk content of rainy cocoon crop and superior silk content of autumn cocoon crop of *A. mylitta*. Sengupta (1986) stated production of better quality cocoons by *A. mylitta* in September-October (Autumn).

The shell weight of Sal reared rainy and autumn crops was higher although total productivity was less (due to low ERR%). Its reason can be determined by studying nutritional values of Sal plants. Anonymous (1968), Jolly (1966) and Jolly *et al.* (1974) described superiority of Sal grown cocoons of *A. mylitta* over Asan and Arjun grown in respect of cocoon toughness and shell weight without any specific mention on their seasonal variablity, variablity of other cocoon crop parameters in different seasons, and the total productivity. Larval rearing on Ber and Sidha in winter gave higher silk productivity than Sal, although the former foodplant is described as secondary foodplant by some previous authors.

Considering overall performances, Sal's rank as a primary foodplant of *A. mylitta* is questionable. Larval rearing on Ber showed significantly (p < 0.05) higher ERR% and also higher silk productivity than Sal with data comparable to Asan and Arjun. Hence we suggest that Ber should be given consideration for rearing and for large scale plantation under different tasar projects involving rearing and plantation programs.

## LITERATURE CITED

Anonymous, 1968. Indian Tasar, Directorate of Commercial Publicity, Government of India, New Dehli, pp. 32.

ANONYMOUS, 1984. A few guidelines to Eri Silkworm Rearing. Regional Sericultural Research Station, Central Silk Board, Titabar, Assam, pp. 6.

JOLLY, M.S., 1966. Tasar Research Scientific Brochure No. 4, Central Tasar Research Station, Central Silk Board, Ranchi, pp. 144.

JOLLY, M.S., S.K. SEN & M.N. AHSAN, 1974. Tasar Culture, 1st Ed. Central SIlk Board, Bombay, pp. 266.

Krishnaswami, S., M.N. Narasimhanna, S.K. Suryanarayan & S. Kumararaj, 1973. Sericulture Manual 2, FAO Agricultural Services Bulletin, Rome, pp. 131.

SARKAR, D.C., 1980. Ericulture in India, 1st Ed. Central Silk Board, Bombay, pp. 51.

SENGUPTA, K. 1986. Tasar Silk Production in India. In: Lectures on Sericulture (Ed. G. Boraiah), Suramya Publishers, Bangalore.

SOKAL, R.R. & F.J. ROHLF, 1969. Biometry: The Principles and practies of Statistics in Biological Research, W.H. Freeman & Co., San Franciso, pp. 776.

TANAKA, Y., 1964. Sericology, Central Silk Board, Bombay, pp. 277.

ULLAL, S.R. & M.N. NARASIMHANNA, 1987. Handbook of practical Sericulture, 3rd Ed. Central Silk Board, Bangalore, p. 166.

YOKOYAMA, T., 1962. Synthesised science of sericulture, Central Silk Board, Bombay, pp. 378.

# The endangered Myrtle's silverspot butterfly: present status and initial conservation planning

Alan E. Launer, Dennis D. Murphy, Jonathan M. Hoekstra and Helen R. Sparrow

Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford CA 94305

**Abstract.** The endangered Myrtle's silverspot butterfly, *Speyeria zerene myrtleae* (Nymphalidae), was studied during a three-year period at the Point Reyes National Seashore and at the site of a proposed resort. Surveys were conducted across much of this insect's historic range. Three large concentrations of Myrtle's silverspot butterflies were identified: two in Point Reyes National Seashore, and one in the coastal prairie and scrub in the vicinity of the Marin-Sonoma county boundary. Continued habitat loss and habitat degradation are the most likely threats. Conservation planning for this butterfly is ongoing, and must include ecosystem management in conjunction with the preservation of suitable habitat.

## INTRODUCTION

On 22 June 1992 the U.S. Fish and Wildlife Service issued a final ruling listing Myrtle's silverspot butterfly (*Speyeria zerene myrtleae* dos Passos and Grey 1945) as an endangered species pursuant to the Endangered Species Act of 1973 (Federal Register 1992). This ruling was deemed justified in order to protect this insect from imminent extinction due to threats resulting from past and proposed habitat loss resulting from residential and commercial development, and from threats due to widespread habitat degradation associated with invasive alien plant species and destructive agricultural practices.

As a consequence of the listing, conservation planning for the Myrtle's silverspot butterfly has become a prime land planning consideration for coastal Marin and Sonoma counties in northern California. While anecdotal data on Myrtle's silverspot butterfly existed at the time of listing, the data were not of sufficient extent or quality to allow comprehensive conservation planning. Specifically, little reliable information existed concerning the number and distribution of Myrtle's silverspot butterfly populations, the approximate number of butterflies in each population, the seasonal phenology, the rates and distances of butterfly dispersal, and the distribution and abundance of larval hostplants and plants that may provide nectar to adults. Without these data conservation activities designed for this butterfly could be oriented at the incorrect spatial and temporal scales, and would not serve to preserve this insect.

While the data shortfall on this subspecies remains profound, this report summarizes recent findings on the biology of Myrtle's silverspot butterfly, and relates these findings to conservation planning for this endangered subspecies.

## Background on Myrtle's silverspot butterfly

Myrtle's silverspot butterfly is a subspecies in the diverse *Speyeria zerene* species complex (dos Passos and Grey 1947, Grey and Moeck 1962, Hammond and McCorkle 1983, McCorkle 1980). Populations of this butterfly species are found scattered across western North America, from the Rocky Mountains west to the coast of central California, and from northwestern Arizona north to southeastern Alaska (Scott 1986). Across this region, *Speyeria zerene* is found in habitats ranging from coastal dune-grassland communities to inland, mid-elevation sagebrush and forest communities. The groups of *Speyeria zerene* populations that have been designated as distinct subspecies are defined primarily on the basis of adult butterfly morphology, geographic distribution, habitat type, and, to a limited extent, inferred phylogenetic affinities (dos Passos and Grey 1945, Grey and Moeck 1962, McCorkle 1980).

Myrtle's silverspot butterfly is thought to be the southernmost entity of a *Speyeria zerene* clade that inhabits the west coast of North America. This group includes the Oregon silverspot butterfly, *Speyeria zerene hippolyta* (protected by the federal Endangered Species Act as a "threatened species"), and Behrens' silverspot butterfly, *Speyeria zerene behrensii* (a candidate for federal protection), as well as Myrtle's silverspot butterfly (Brittnacher *et al.* 1978, dos Passos and Grey 1945, Grey and Moeck 1962, McCorkle 1980). Populations of Myrtle's silverspot butterfly formerly were found in dunes and bluffs from coastal San Mateo County in the south, to the vicinity of Jenner Beach (Sonoma County) in the north (Steiner 1990) (Map 1). Populations of *Speyeria zerene* butterflies containing individuals phenotypically intermediate between Myrtle's silverspot butterfly and Behrens' silverspot butterfly were known to exist north of Jenner Beach and south of Anchor Bay (Mendocino County).

By the late 1970s Myrtle's silverspot butterfly populations south of the Golden Gate were thought to be extinct, and the butterfly was considered to still be thriving only at the Point Reyes National Seashore. In 1990, Myrtle's silverspot butterflies were observed in the coastal grasslands north of Estero de San Antonio, at the site of the proposed Marin Coast Golf Ranch (Arnold 1990). This observation triggered studies at the proposed resort site and throughout the historic range of the butterfly. Starting in 1991, extensive field studies on Myrtle's silverspot butterflies were conducted by researchers from the Center for Conservation Biology at Stanford University. These studies were expanded to include field work at Point Reyes National Seashore in 1992.

## Conservation planning for Myrtle's silverspot butterfly

Concurrent with federal protection under the Endangered Species Act, conservation planning for Myrtle's silverspot butterfly was initiated on two different levels. Site-specific information on potential impacts construction would have on the butterfly was required at the 510 hectare Marin Coast Golf Ranch (MCGR). On a more general level, baseline
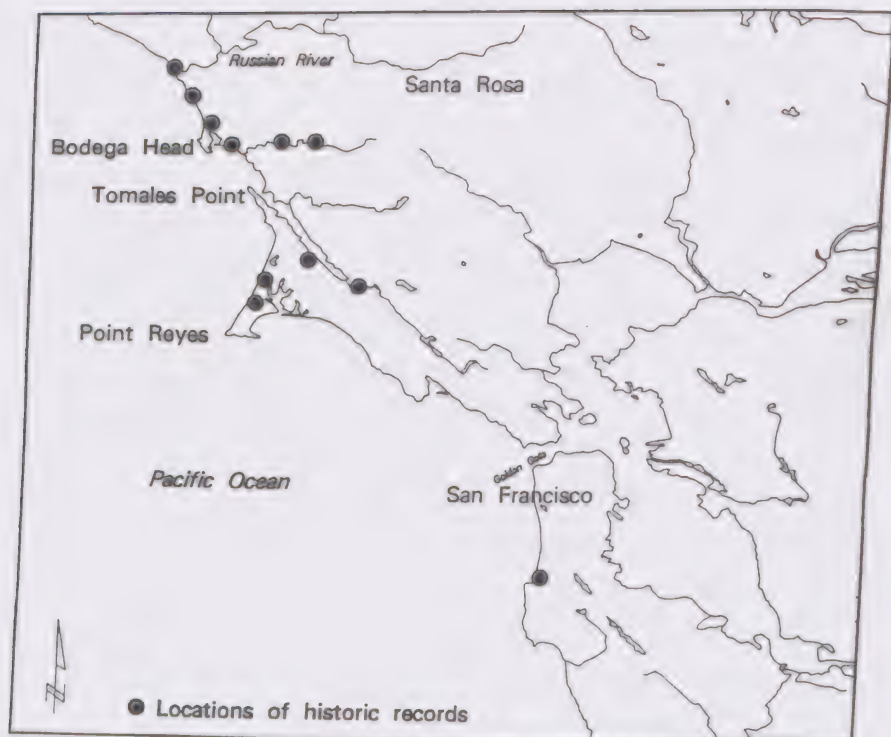
Figure 1. Distribution of historic collection sites of Myrtle's silverspot butterfly (after Steiner 1990, and numerous communications with local lepidopterists). Note that the type locality, San Mateo California (dos Passos and Grey 1945), could refer to either the county of San Mateo, including Pacific coastal areas known historically to support the butterfly, or to the town of San Mateo, located on the bay-side of the San Francisco Peninsula — an area we consider unlikely to have historically supported a Myrtle's silverspot butterfly population. For this report, the source of the type specimens is considered to be coastal San Mateo County, probably in the vicinity of the town of Pacifica. Also note that the zerene butterflies from the vicinity of Jenner are occasionally considered intermediate between *S. z. myrtleae* and *S. z. behrensii.* (Map was created using ARC/INFO and the Digital Chart of the World.)

information on broad patterns of distribution and abundance within the approximately 28,500 hectare Point Reyes National Seashore (PRNS) was needed to determine the status of the insect within the reserve and to determine if a management plan specifically designed to protect the butterfly was warranted. While these two planning efforts were different in breadth and, to some extent, conservation orientation, it was evident at the onset that both projects required field activities to address the shortfall of reliable data.

Information on the site-specific distribution and abundance, including measures of both relative and absolute abundance of adult butterflies, larval hostplants, and plants potentially providing nectar was needed for preliminary planning at the proposed MCGR. Also needed for initial planning at the MCGR site was information on butterfly dispersal and phenology, and on the status of the butterfly in surrounding regions. Off-site surveys were considered necessary in order to put site-specifiic information into a proper regional context, because on-site conservation planning is strongly dependent on the target organism's local and regional status. For the second phase of conservation planning at the MCGR, precise information was needed on the spatial distribution of the butterfly in areas where development was proposed, for purposes of the design of management activities.

At Point Reyes National Seashore baseline information on distribution and abundance of the butterfly was lacking. Myrtle's silverspot butterfly was known to occur in several locations at the Seashore, but much of the Seashore had not been surveyed. Along with baseline information, the development of a long-term monitoring scheme and management options were initiated.

## METHODS

Beginning April 1991 and continuing through September 1993, field activities were conducted on 115 days (including portions of 245 person-days). Most of the work centered on two locations, the Point Reyes National Seashore and the site of the proposed Marin Coast Golf Resort. On twenty days during the peak adult butterfly flight periods (as determined by on-going work at PRNS and the MCGR), surveys for Myrtle's silverspot butterflies were conducted in numerous locations throughout the recent range of the butterfly (survey sites distributed from the vicinity of Jenner Beach to the southern coast of Tomales Bay).

Mark-recapture activities were conducted during two seasons, in 1991 at the MCGR and in 1993 at PRNS. These activities were conducted according to the techniques described in Ehrlich and Davidson (1960). This method has been found to have no lasting impacts on comparatively large and robust butterflies, such as Myrtle's silverspot butterfly (Orive and Baughman 1989, but see Murphy 1988 for caveats). At the time of capture each butterfly was individually marked, sexed, and scored for wing wear (a measure of age). Data were analyzed using a Jolly-Seber population estimation program. The mark-recapture study was designed to be the first step in delineating population boundaries and in estimating the absolute number of Myrtle's silverspot butterflies at each of the two primary study sites. The timing of adult butterfly emergence was estimated on the basis of condition at first capture (individuals scored as wear condition 0.5 were assumed to have eclosed within two days of capture, individuals of condition 1.0 were assumed to have eclosed three to five days prior to capture, etc.).

The MCGR site was divided into 15 subareas, each approximately 35 hectares in extent (Launer and Murphy 1991). These subareas roughly corresponded to topographic features at the site. In 1991, each of these subareas was used as a focal point for the mark-recapture study. In addition to the mark-recapture activities, the amount of time spent in each subarea, and the number of

butterflies handled or observed but not handled (used as an estimate of non-captured butterflies) were recorded in order to calculate a relative measure of butterfly abundance (butterflies per observer-hour). In 1992 and 1993, kilometer-long transects were located in each of the 15 subareas in an effort to quantify relative abundance (Pollard and Yates 1993). Transects were designed to be representative of the topographic and biotic diversity present in each of the subareas. Transects were walked at a consistent pace on five occasions during periods of appropriate weather during both the 1992 and 1993 seasons. Transect walks were designed to be conducted weekly during peak butterfly flight period, but inclement weather eliminated some periods, hence the mean time between sampling periods was approximately ten days in 1992 and four days in 1993. All butterflies observed within five meters and in front of field workers were counted; those butterflies either behind observers or farther than five meters distant were not counted (Launer and Murphy 1992).

At PRNS, the 1993 mark-recapture study was centered at the dune-scrub interface located at North Beach. In this area, comparatively large numbers of butterflies were observed in 1992 visiting the abundant wildflowers (*Grindelia rubicaulis, Abronia latifolia, Monardella undulata*, and *Erigeron glaucus*) (Sparrow and Launer 1992). To the east of the North Beach site, in scrub and grassland communities, Myrtle's silverspot butterflies were observed on occasion, but were too dispersed to be effectively included in the mark-recapture study.

In 1991, prior to federal protection, voucher specimens from the MCGR were retained on a weekly basis. On average, five specimens were collected each week during the study period, and were taken only after it was apparent that the population at the site consisted of several thousands of individuals. Sampling at this low intensity is thought to be of negligible impact to butterfly populations (Harrison *et al.* 1991).

## RESULTS AND DISCUSSION
### Distribution

Surveys documented Myrtle's silverspot butterflies in two broad areas at Point Reyes National Seashore and at the proposed Marin Coast Golf Ranch site (Map 2). Surveys also documented Myrtle's silverspot butterflies in locations surrounding the MCGR, including Estero Lane (Sonoma County), Estero Road (Marin County), and the hills between Dillon Beach and Estero de San Antonio (Marin County). No Myrtle's silverspot butterflies were observed at any other survey sites. While the results of these surveys should not be taken as conclusive evidence of absence of the subspecies from areas where they were not observed, it is unlikely that large concentrations of Myrtle's silverspot butterflies, such as those observed at PRNS and at MCGR, exist in publicly accessible areas located between Jenner Beach and the Bodega Bay Golf Course, or in areas located between Dillon Beach and Point Reyes Station. There are, however, inaccessible private landholdings in the coastal region that appear to be capable of supporting Myrtle's silverspot butterflies, and unknown populations of the butterfly inland could also exist.

At PRNS, Myrtle's silverspot butterflies were found at the Tomales Point tule elk range and throughout the bluffs, hills, grasslands, and
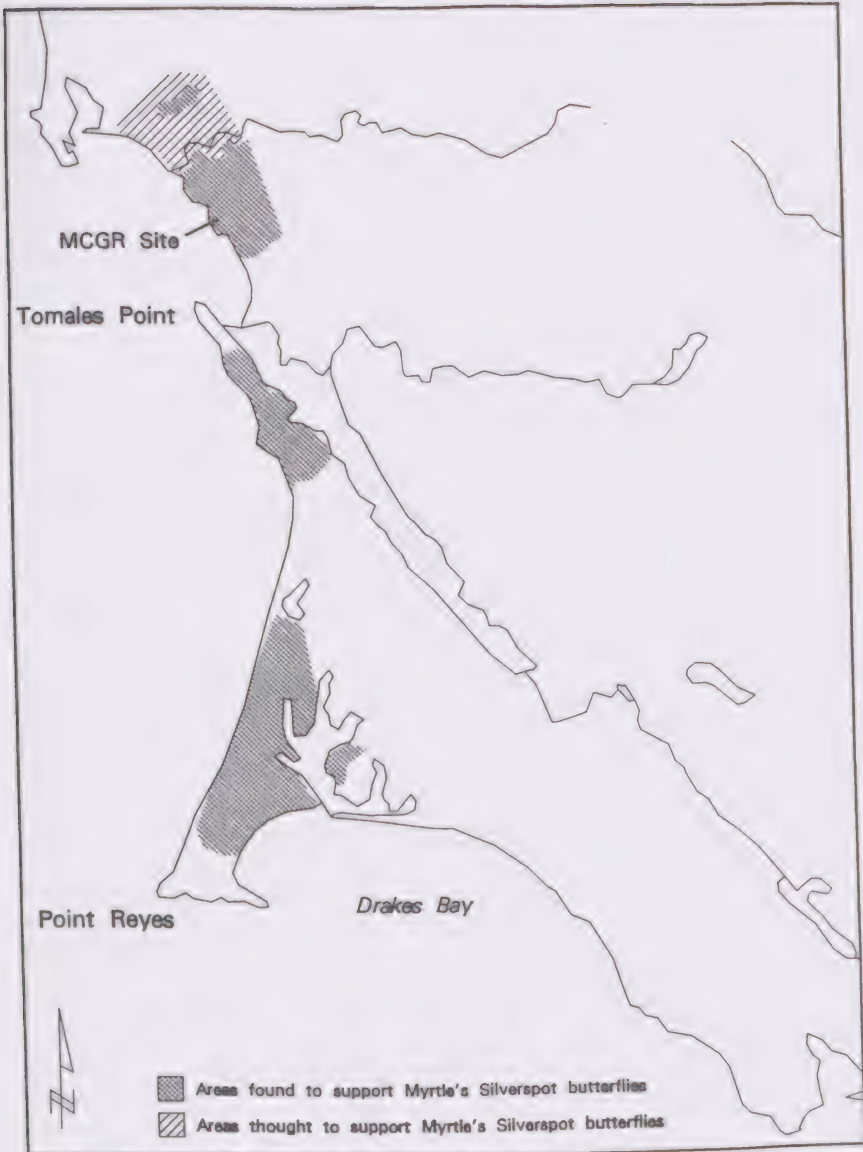
Figure 2. Present distribution of Myrtle's silverspot butterfly. (Map was created using ARC/INFO and the Digital Chart of the World.)

back-dunes west of Drakes Estero and Schooner Bay (Map 2) . Within each of these two areas, butterflies were found in varying abundances — high concentrations were associated with locations protected from the frequent winds, or with areas supporting large numbers of plants that potentially provide nectar.

Myrtle's silverspot butterflies were unevenly distributed across the MCGR site. Most of the butterflies were recorded from two areas — an approximately 2.5 kilometer coastal drainage system forming part of the northern boundary of the site (and including adjacent off-site areas), and along the Estero de San Antonio. This distribution was consistent in 1991 and 1992. In 1993, a slight shift in distribution was observed that included an expansion by the butterflies into a subarea that had been sparsely occupied in previous years. This slight expansion may have been related to an apparent increase in the density of bull thistles in the newly occupied subarea, but such a causal relationship can only be inferred.

### Estimated number of Myrtle's silverspot butterflies

At Point Reyes National Seashore (North Beach) in 1993, 76 Myrtle's silverspot butterflies were marked (38 males and 38 females), and 24 recaptures were recorded. The low numbers of recaptures is problematic for several of the algorithms used by Jolly-Seber population estimation programs, and eliminates the possibility of a precise population estimate. However, if changes in daily population levels are assumed to be fairly consistent and calculations are made using a range of Scott's average phi values (in this case, the data indicated a range of average phi values from 0.2 to .06), a fairly reliable estimate can be derived. Using these corrections, between 200 to 600 individual butterflies were estimated to visiting the back-dune areas adjacent to North Beach in 1993.

The estimate of between 200 to 600 individual butterflies should not be taken as an estimate of overall population size in central Point Reyes since we were unable to delineate spatial boundaries of the population, and it is probable that the butterflies visiting the nectar sources at North Beach constitute only a fraction of an extended population. Based on the mark-recapture study and on extensive observations, it is likely that more than 1,000 butterflies but fewer than 5,000 butterflies were present in central Point Reyes in 1993.

At the Marin Coast Golf Ranch site in 1991, 255 Myrtle's silverspot butterflies were marked and then released. Unfortunately, only 19 recaptures were recorded (this low number of recaptures is even more surprising considering that 120 additional observations of unmarked butterflies were recorded out of the context of the mark-recapture study). Again, the comparatively small number recaptures precludes a precise estimate of the total number of butterflies present on the MCGR site in 1991, but it suggests that the effort sampled a large and open population. After considering a number of factors including the length of the adult butterfly flight season, the number of recaptured individuals in relation to the number of marked butterflies, butterfly wear rates, and apparent limitations to butterfly dispersal, a conservative estimate of between 2,500 and 5,000 adult Myrtle's silverspot butterflies are thought to have resided at the proposed resort site in 1991.

## Phenology of Myrtle's silverspot butterfly

Onset of the adult butterfly flight season varied between years and between sites. In 1991 adult butterflies were estimated to have begun emerging during the second week of July at the Marin Coast Golf Resort. In contrast, both the 1992 and 1993 adult butterfly flight seasons at the MCGR were projected to have begun in late June. During 1991 to 1993 at Point Reyes National Seashore, the onset of the Myrtle's silverspot butterfly flight season was apparently initiated in mid- to late June. In general, onset of Myrtle's silverspot butterfly flight season was one to two weeks earlier at PRNS than at MCGR. It should be noted that across the Bay area in 1991 many phenological events were exceptionally late — butterfly flight seasons and plant flowering periods were documented as comparatively delayed (for example, the 1991 onset of the Bay checkerspot butterfly flight period at Stanford University's Jasper Ridge was the latest recorded in 33 years of population censusing).

Adult butterflies were present continuously at the two primary study sites for at least two months each year, and in 1991 butterflies were last observed on the MCGR site on 5 October — indicating a three month flight season. During the two to three month flight period, a number of demographic shifts were evident, and large numbers of adult butterflies were observed from the second week of July until mid- to late August. Although individuals of both sexes were found together throughout the flight season, an approximate ten day difference in the peak flight times of the two sexes was apparent; adult male butterflies appeared to reach peak abundance in late July, while adult female butterfly abundance appeared to peak during the first two weeks of August. Note again that 1991 was probably an exceptional year, and peak abundances were not reached until 20 August for males and 1 September for females. The extended flight season exhibited by Myrtle's silverspot butterflies is consistent with other Lepidoptera inhabiting coastal areas (Hammond and McCorkle 1983, Langston 1974). Weather at the primary study sites strongly impacts adult butterfly activity. While butterflies were invariably active during periods of overcast, but calm weather, they ceased to be active during periods of foggy and windy weather. Such inclement weather conditions frequently occurred: indeed, during the three-year study period no adult butterfly activity at all was noted on more than 25% of the days during the adult flight season, and butterfly activity was minimal on many of the remaining days. Days of weather sufficiently mild as to allow for complete days of butterfly activity were uncommon, and most days had only a three or four hour period when the butterflies were active.

### Habitat

The habitat of the Myrtle's silverspot butterfly has been considered to include only low elevation dune and grassland areas immediately inland from the coast. This habitat is well within the summer "fog belt," a

physical setting that ensures comparatively buffered environmental conditions. Coastal bluff grasslands and scrub at higher elevations were not considered to serve as primary habitat for the Myrtle's silverspot butterfly. However, work at the Marin Coast Golf Ranch site and at Point Reyes National Seashore determined that grasslands and small valleys located amidst rolling hills may be densely populated by the butterfly. In particular, areas protected from the persistent wind, up to five kilometers from the coast and up to 250 meters in elevation, were found to support substantial numbers of adult butterflies.

*Viola adunca*, the presumed larval hostplant, is patchily distributed throughout the r ion, and inhabits a range of biological communities, including grassland, scrub, and dune plant communities. The presence of *Viola adunca*, therefore, is not a reliable predictor of the presence of Myrtle's silverspot butterflies. Determinations of habitat suitability must be based on multiple factors, including, but not limited to, distribution of larval hostplants.

The plant species available that potentially provide nectar differ between the upland and dune habitat areas. In the grassy uplands, especially those subject to grazing by livestock, native plant species potentially providing nectar are generally scarce. Butterflies were frequently observed visiting bull thistle, *Circium vulgare*. This alien species is widespread in disturbed areas, along roads and fencelines, and in comparatively moist areas. Another alien plant species, Italian thistle (*Carduus pycnocephalus*), is also abundant in disturbed areas (particularly overgrazed areas), and was visited by butterflies that were active before mid-July. In upland areas, very few visits to native plant species were observed. At PRNS, *Grindelia* (probably *G. rubicaulis*) and *Monardella* (probably *M. villosa*) were occasionally visited, and at the MCGR, *Monardella villosa* was visited. At the dune-scrub interface in central PRNS, *Grindelia rubicaulis*, *Abronia latifolia*, and *Monardella undulata* were visited regularly by Myrtle's silverspot butterflies. In this zone, *Grindelia* and *Abronia* are found in dense patches up to several meters in diameter. Butterflies frequented these large patches. *Erigeron glaucus* was visited to lesser degree. *Circium vulgare* was rarely visited by Myrtle's silverspot butterflies in the dune-scrub zone. Flowers of the invasive iceplant (*Mesembryanthemum* species) were never visited by Myrtle's silverspot butterflies.

The availability of nectar is potentially a critical factor for the long-term persistence of Myrtle's silverspot butterfly populations. In a related species, *Speyeria mormonia*, a strong correlation exists between the amount of nectar consumed by female butterflies and the number of eggs they produce (Boggs and Ross 1993). This implies that under field conditions, reduced nectar availability can limit the total number of eggs produced, and can result in a reduction in the number of offspring that survive to become adults in the subsequent year (assuming that there is negligible density dependent mortality of larvae). Widespread overgraz-

ing in the region may have substantially reduced the availability of nectar (particularly native plant species), and could be contributing to a regional decline of the butterfly.

## Adult butterfly dispersal and the spatial scale of Myrtle's silverspot butterfly populations

At the Marin Coast Golf Ranch site in 1991, few butterflies were recaptured in subareas different from those of their initial capture. Slightly more than 50% (10 of 19) of recaptured butterflies were taken in the same subarea as initially recorded, and 95% (18 of 19) of all recaptures were made in either the same subarea as initial capture or in an immediately adjacent subarea. Only 5% (1 of 19) of butterflies captured more than once dispersed to a non-adjacent subarea. The mean distance traveled by all recaptured individuals was approximately 75 meters (the mean value for distance moved between recapture events is based on distance between center points of the subareas). Of those butterflies documented to have moved into a different subarea, the mean distance traveled was approximately 350 meters, and the longest recorded movement was approximately 1,500 meters.

When these results from the mark-recapture study are coupled with the extensive observations at the proposed resort site during the three study years, it appears that Myrtle's silverspot butterflies generally stayed within circumscribed topographic units — coastal drainage systems separated by wind-swept ridges and exposed grasslands. Within these protected areas, daily movements of several hundred meters are undoubtedly frequent, and longer movements, up to and likely exceeding the 1,500 meters recorded by the mark-recapture study, are not unusual.

Dispersal between the two "large" drainage systems at the MCGR site was not recorded during the course of this study. However, given the vagility of the butterflies, and the comparatively short distances between drainages, it is probable that dispersal between drainage systems does occur.

At the dune-scrub interface at Point Reyes, high concentrations of nectar-producing plants attract butterflies from unknown and perhaps distant natal areas; observations imply movements on the order of several kilometers. During 1992 and 1993, there were numerous observations of butterflies flying without stopping through the grasslands and scrub east of North Beach, and across the main road. While conclusive proof of movements between distant population centers would be desirable, the practicalities of conducting a mark-recapture study in areas supporting low butterfly densities eliminated this option.

The balanced sex ratio observed at North Beach in 1993 (50:50) may indicate that only a subset of a population was sampled. In general, female butterflies are less likely to be encountered, hence captured, than are male butterflies, and mark-recapture studies nearly always involve the handling of more males than females (Ehrlich *et al.* 1984). The few

instances in which more females than males are captured typically occur when sampling is restricted to the end of the flight season (butterflies, and *Speyeria* in particular, are generally protandrous), or when sampling occurs where scarce resources attract disproportionate numbers of females from surrounding areas. The first possibility is unlikely in this case; the timing of the 1993 study indicates that females may have been undersampled. It is probable that the North Beach study site represents just a portion of the geographic range of an open and highly dispersed Myrtle's silverspot butterfly population residing in central Point Reyes.

While conclusive determination on the geographic extent of Myrtle's silverspot butterfly populations is lacking, these studies indicate that it is probable that at least three demographically independent populations of Myrtle's silverspot butterflies exist: central Point Reyes (including areas in the vicinity of North Beach, South Beach, and Drake's Beach); Tomales Point (within the PRNS tule elk range); and in the vicinity of the MCGR (this population probably extends north to Estero Lane in Sonoma County). It is unclear the degree to which these ostensible populations, particularly those located at MCGR and central PRNS, are subdivided, but it is likely that substantial interchange of individuals occurs between areas of high butterfly density within each of the three areas. Similarly diffuse populations of this approximate geographic scale have been suggested previously for the Oregon silverspot butterfly (Pickering *et al.* 1991, Pickering *et al.* 1992).

## CONCLUSIONS AND RECOMMENDATIONS

Species-specific conservation planning is never an easy task, but working with an invertebrate species presents an especially daunting set of challenges — particularly when the available period of investigation is limited (New 1991, Pollard and Yates 1993). Distribution and abundance "snap-shots" of butterfly populations and metapopulations, that is studies based on single or two consecutive field seasons, need to be viewed in the context of dynamic natural fluctuations typical of such systems (Baughman and Murphy 1990). In light of the lack of a historic perspective, the precise status of *Speyeria zerene myrtleae* remains largely unresolved. It is fairly certain that this butterfly has declined in distribution and in abundance; and even with the large number of butterflies inhabiting the nominally protected lands of Point Reyes National Seashore, this butterfly warrants the protection it has been afforded under the Endangered Species Act. However, considering the large extent of generally inaccessible private land in the region, there may be undiscovered populations of Myrtle's silverspot butterflies scattered across coastal Marin and Sonoma Counties. It is doubtful that any populations of Myrtle's silverspot butterfly exist south of the Golden Gate. It is also possible that inland populations of Myrtle's silverspot butterflies exist since the ecologically similar Oregon silverspot butterfly, *Speyeria zerene hippolyta*, is present at Mount Hebo, a site well away from the coast.

At Point Reyes National Seashore, the distribution and abundance of the butterfly indicate it is not in immediate danger of extinction, and that even without conservation actions specifically targeting the butterfly, this subspecies will likely persist within the park for some time to come — an observation that suggests that design and implementation of management activities need not be carried out under the "crisis management" timetable so frequent to conservation efforts. Long-term persistence of Myrtle's silverspot butterfly, however, is not guaranteed because the cumulative impacts of grazing (from both domestic livestock and tule elk), invasive alien plant species, and possibly the suppression of natural disturbances, are not well understood. The region-wide decline of the butterfly implies that such cumulative impacts have been significant and may eventually threaten the existence of the butterfly even at PRNS.

The ecosystems of coastal California, including PRNS, have been altered significantly by more than one hundred years of human activities and by the invasions of alien plant and animal species. Unfortunately, the impacts of these activities are likely so pervasive that complete cessation of some commercial ventures, specifically grazing, would probably lead to the loss of native species as non-native species slowly eliminate them (Davis and Sherman 1992, Elliott and Wehausen 1974, Hardham and True 1972, Hektner and Foin 1974). With this virtually permanent alteration of the habitats that support Myrtle's silverspot butterfly comes the necessity of long-term management — simply setting aside land for butterfly reserves with no active management will be insufficient for the conservation of this insect. Perhaps the most important of the management options is the identification of grazing regimes that are beneficial to larval hostplants and plants providing nectar resources, and conservation planning for Myrtle's silverspot butterfly should include scientifically defensible grazing and habitat restoration experiments. As it is inconceivable that one grazing regime will prove optimal for all components of biotic diversity in the region, and because many effects of grazing may not be apparent for many years, long-term conservation planning at PRNS should incorporate areas subjected to range of grazing pressures — from no livestock to comparatively high densities of livestock.

Unfortunately, managed grazing will not be a complete solution. In the back-dune areas, use of grazing to minimize the impacts of non-native species, particularly iceplant, will not be appropriate. It is unlikely that native plant species dwelling on the physically loose substrates of the dune areas would benefit from livestock, and such disruption could exacerbate the transition from native to non-native plant species. In that these dune communities apparently provide nectar resources critical to the long-term persistence of Myrtle's silverspot butterflies, programs of iceplant control and dune restoration need to be initiated. With the reality that iceplant will not be eliminated from PRNS in the foreseeable future (if ever), areas still supporting comparatively high densities of

native plant species, such as the back-dunes at North Beach, need to be focal points of such control and restoration efforts.

Another apparent conservation problem faced by Myrtle's silverspot butterfly is the collection of specimens. While it is very doubtful that collection of specimens has ever constituted a threat to any Myrtle's silverspot butterfly population, areas where comparatively high concentrations of female butterflies can be found, such as North Beach at PRNS, should be patrolled during the adult butterfly flight season to discourage poaching.

At the proposed Marin Coast Golf Ranch, studies indicate that Myrtle's silverspot butterflies are more or less absent from a sizable portion of the site, hence development of some areas could have a negligible impact on the butterfly. However, a problem for site-specific conservation efforts designed for the butterfly is that the MCGR site constitutes only a portion of the distribution of a widespread butterfly population. This is a near universal problem with site-specific planning in that most butterfly populations are not encompassed in their entirety by political or human-defined boundaries. As a result, site-specific planning efforts tend to focus on just portions of populations, and adjacent off-site areas that are critical to the long-term persistence of target species, may not benefit from conservation planning. Given the extent of private-sector conservation planning, this problem is unlikely to be resolved with any strategy short of a full regional habitat conservation plan — something that often is suggested, but rarely accomplished.

A common theme for conservation planning for butterflies is that planning increasingly focuses on proper ecosystem management — as reserve design options in urban and suburban areas dwindle, the development of resource management plans are taking center stage. Across California early conservation efforts designed to protect the state's threatened butterflies focused on reserve design, but the last decade has seen a shift toward ecosystem management — gorse removal on San Bruno Mountain for Mission blue butterflies, iceplant control for Smith's blue butterflies, buckwheat outplanting for El Segundo blues and Lange's metalmarks, and phased grazing for Bay checkerspot butterflies. Without the the implementation of management activities — phased grazing in grassland and scrub areas, and iceplant control in back-dune areas — lands set aside for Myrtle's silverspot butterfly will likely degrade and the butterfly well might continue to decline.

## LITERATURE CITED

ARNOLD, R. A. 1990. Unpublished report to Harding Lawson Associates (Novato,
    California).

BAUGHMAN, J. F. & D. D. MURPHY. 1990. Beware of snapshots at the bottleneck
    — temporal considerations in conservation planning. Endangered Species
    Update 7 (8 & 9): 6.

BOGGS, C. L., & C. L. ROSS. 1993. The effect of adult food limitation on life history
    traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74: 433-
    441.

BRITTNACHER, J. G., S. R. SIMS, & F. J. AYALA. 1978. Genetic differentiation
    between species of the genus *Speyeria* (Lepidoptera: Nymphalidae). Evolution
    32: 199-210.

DAVIS, L. H. & R. J. SHERMAN. 1992. Ecological study of the rare *Chorizanthe
    valida* (Polygonaceae) at Point Reyes National Seashore, California. Madrono
    39: 271-280.

DOS PASSOS, C. F. & L. P. GREY. 1945. A new species and some new subspecies of
    *Speyeria* (Lepidoptera, Nymphalidae). American Museum Novitates 1297:
    1-17.

———. 1947. Systematic catgalogue of *Speyeria* (Lepidoptera, Nymphalidae) with
    designations of types and fixations of type localities. American Museum
    Novitates 1370: 1-30.

EHRLICH, P. R. & S. E. DAVIDSON. 1960. Techniques for capture-recapture studies
    of Lepidoptera populations. Journal of the Lepidopterists' Society 14: 227-
    229.

EHRLICH, P. R., A. E. LAUNER, & D. D. MURPHY. 1984. Can sex ratio be defined or
    determined? The case of a population of checkerspot butterflies. The American
    Naturalist 124: 527-539.

ELLIOTT, H. W. III, & J. D. WEHAUSEN. 1974. Vegetational succession of coastal
    rangeland of Point Reyes Peninsula. Madrono 22: 231-238.

FEDERAL REGISTER. 1992. Endangered and threatened wildlife and plants; six
    plants and Myrtle's silverspot butterfly from coastal dunes in northern and
    central California determined to be endangered. 57: 27848-27858.

GREY, L. P. & A. H. MOECK. 1962. Notes on overlapping subspecies. I. An example
    in *Speyeria zerene* (Nymphalidae). Journal of the Lepidopterists' Society 16:
    81-97.

HAMMOND, P. C., & D. V. McCORKLE. 1983. The decline and extinction of *Speyeria*
    populations resulting from human environmental disturbances
    (Nymphalidae: Agrynninae). The Journal of Research on the Lepidoptera
    22: 217-224.

HARDHAM, C. B. & G. H. TRUE JR. 1972. A floristic study of Point Arena,
    Mendocino County, California. Madrono 21: 499-504.

HARRISON, S., J. F. QUINN, J. F. BAUGHMAN, D. D. MURPHY, & P. R. EHRLICH. 1991.
    Estimating the effects of scientific studies on two butterfly populations. The
    American Naturalist 137: 227-243.

HEKTNER, M. M. & T. C. FOIN. 1977. Vegetation analysis of a northern California coastal prairie: Sea Ranch, Sonoma County, California. Madrono 24: 83-103.

LANGSTON, R. L. 1974. Extended flight periods of coastal and dune butterflies in California. The Journal of Research on the Lepidoptera 13: 83-98.

LAUNER, A. E. & D. D. MURPHY. 1991. Unpublished report submitted to Marin County (via Marin Coast Associates).

———. 1992. Unpublished report submitted to Marin County (via Marin Coast Associates).

McCORKLE, D. V. (WITH P. C. HAMMOND & G. PENINGTON). 1980. Ecological investigation report: Oregon silverspot butterfly (*Speyeria zerene hippolyta*). Unpublished report submitted to Siuslaw National Forest. 117 pages.

McCORKLE, D. V. & P. C. HAMMOND. 1988. Biology of *Speyeria zerene hippolyta* (Nymphalidae) in a marine-modified environment. Journal of the Lepidoterists' Society 42: 184-195.

MURPHY, D. D. 1988. Are we studying our endangered butterflies to death? The Journal of Research on the Lepidoptera 26: 236-239.

NEW, T. R. 1991. Butterfly conservation. Oxford University Press Australia: Melbourne. 224 pages.

ORIVE, M. E. & J. F. BAUGHMAN. 1989. Effects of handling on *Euphydryas editha* (Nymphalidae). Journal of the Lepidopterists' Society 43: 244-247.

PICKERING, D., C. MACDONALD, & N. RUDD (The Nature Conservancy). 1992. Population dynamics and adult behavior of the Oregon silverspot butterfly *Speyeria zerene hippolyta* (Lepidoptera, Nymphalidae). Unpublished report to the Siuslaw National Forest. 60 pages.

PICKERING, D., D. SALZER, & C. MACDONALD (The Nature Conservancy). 1991. Population dynamics and habitat characteristics of the Oregon silverspot butterfly *Speyeria zerene hippolyta* (Lepidoptera, Nymphalidae). Unpublished report to the Siuslaw National Forest. 99 pages.

POLLARD, E. & T. J. YATES. 1993. Monitoring butterflies for ecology and conservation. The British butterfly monitoring scheme. Chapman and Hall: London. 274 pages.

SCOTT, J. A. 1986. The butterflies of North America. Stanford University Press: Stanford. 583 pages.

SPARROW, H. & A. E. LAUNER. 1992. Unpublished report submitted to Point Reyes National Seashore.

STEINER, J. 1990. Bay Area butterflies: the distribution and natural history of San Francisco region Rhopalcera. Unpublished master of science thesis (C.S.U. Hayward).

## Book Reviews

KEEPING AND BREEDING BUTTERFLIES AND OTHER EXOTICA: PRAY-
ING MANTISES, SCORPIONS, STICK INSECTS, LEAF INSECTS, LOCUSTS,
LARGE SPIDERS, AND LEAF-CUTTER ANTS. John L. S. Stone. 1992. Blandford,
London (distributed in the U.S. by Sterling Publishing Co., Inc., 387 Park Avenue
South, New York, NY 10016-8810). 192 pp., 16 pp. of color photographs, numer-
ous B & W photographs & line drawings. Hardcover, 14.5 x 22.5 cm, ISBN 0-7137-
2293-2. $24.95.

Judging from this book's title and length, I had hoped for a useful book advising
on rearing butterflies and other arthropods. Unfortunately, I was disappointed.

The book begins with a very brief Introduction and Preface. The body is divided
into four parts: Butterflies of Temperate Regions, Some Migratory Butterflies,
Breeding Butterflies, and Breeding Other Exotica. I will treat the first two parts
of the book separately from the last two, since they are really more like two
different books.

The first section, Butterflies of Temperate Regions, treats only British butter-
flies. This section would be useful if it actually provided rearing advice for the 58
British species treated. Instead, the discussion for each species includes three
sections: Distribution (global distribution of the species), Foodplants (accepted
larval hostplants in Britain), and General Notes. For each species, the General
Notes section deals almost entirely with British distribution, habitats and timing
of broods; their overwintering stage; a brief description of each species' larvae and
pupae; and how to identify the adults (nearly one whole page is devoted to the
identification of the three British subspecies of *Coenonympha tullia* !). Larval
behavior is often noted. I had expected tips on how to rear each species in the
General Notes section, but found no hints until p. 33, where Stone warns the
reader to separate larvae of *Anthocharis cardamines* , due to their cannibalistic
tendencies. Some of the information in this section is too vague to be of much use.
For example, on page 80, under the Foodplants section for *Mellicta athalia* , Stone
lists four known foodplants, then states "A number of other plants are also
reported, including some garden plants." What are these other hostplants? In a
book about rearing butterflies that treats only British species, I would expect as
complete a list of known larval hostplants as possible, especially if some of these
may be available in my own garden, or as naturalized wild plants in North
America! The second section, Some Migratory Butterflies, only treats migrant
species that occasionally reach Britain. The format of this section is very similar
to that of the first section.

The contents of the first two sections of this book seem unrelated to the title.
My frustration with the book was strengthened each time I came across a
mistake. A careful examination of the text by several reviewers should have been
made before publication, so that the numerous mistakes scattered throughout
the text could have been found and corrected (only one reviewer is mentioned in
the Acknowledgments ).

The 16 color plates that are inserted between the text of section one are quite
nice, and include many of the rearing tips found in that section. The plates make
the book much more attractive overall. However, there are several species

(*Triodes* sp., *Cressida cressida* , *Caligo brasilensis* , and *Zerinthia polyxena* )
pictured on the color plates that receive no mention anywhere in the text, making
me wonder why they were included. The color plates are not without mistakes,
unfortunately, as can be seen by the mimic female *Hypolimnas misippus* that is
labeled as its model, *Danaus chrysippus* .

The real value of this book is in the third and fourth sections (final 84 pp.). The
third section, Breeding Butterflies, consists of four parts (General Information,
Housing For Captive Breeding, Breeding Methods For Some Tropical Species,
and Breeding Methods For Exotic Species). This section begins by providing
general information about butterfly life history, and continues with a discussion
of various breeding cages; it does provide some excellent tips on how to rear
butterflies in captivity, and may be useful to anyone who desires to grow large
numbers of butterflies. The part of section three dealing with the rearing of exotic
species is less useful, for it proclaims too many broad generalities. For example,
Stone asserts that for papilionids, "The two main foodplants are *Citrus* and
*Aristolochia* ." Very intricate details are, however, presented in the discussion of
breeding *Heliconius* butterflies. The fourth section, Breeding Other Exotica, also
gives advice that may be useful to anyone wishing to rear Praying Mantids,
Scorpions, Stick Insects, Leaf Insects, Locusts, Large Spiders, or Leaf-Cutter
ants.

I was surprised that no mention of rearing moths was made, especially of the
commonly grown *Saturnia pavonia* , which occurs throughout Europe (including
Britain). The text was difficult to read- often wordy, disorganized, and very
opinionated, as where Stone states that "Heliconid butterflies are, without a
doubt, *the* most rewarding species to breed," and where he describes papilionids
as being the "largest and most beautiful butterflies." There are several sections
in the book where very little useful information is presented. Many of the
"scientific facts" are of questionable validity, as can be seen in the introduction
to section two where Stone explains that some butterflies "seem to enjoy flying
great distances." The writing style gives the text a very unprofessional tone.
Much of the useful rearing advice must be gleaned from his numerous personal
stories. The absence of a bibliography (although there is a suggested reading list
that fails to mention any book dealing primarily with rearing arthropods)
suggests that Stone did very little research, and also reinforces my impression
that the facts about arthropods given in this book are primarily Stone's own
observations.

I cannot recommend this book to a very wide audience. It may be useful to
anyone wishing to find and rear British butterflies, or to persons planning to
breed butterflies or other arthropods for a butterfly house or other living exhibit.
To anyone else, this book would be of limited use, and another book dealing only
with rearing techniques would be a better alternative for the price.

*Andrew D. Warren*, *Department of Entomology, Comstock Hall, Cornell
University, Ithaca, NY 14853-0999*

TINEID GENERA OF AUSTRALIA (LEPIDOPTERA). 1993. G. S. Robinson and E. S. Nielsen. Monographs on Australian Lepidoptera: Volume 2, 344 pp +xvi. CSIRO Publications, East Melbourne. $US80. Hardbound.

Australia may be a large country with a small population, but on a per capita basis Aussies clearly lead the world in producing serious, meticulous, works that have established new standards to define contemporary systematics of the Lepidoptera. This second volume of the Monographs on Australian Lepidoptera series deals with all 44 genera of the family Tineidae known to occur in Australia. In the global context there are about 3500 species in 320 genera. Among the 44 Australian genera, 9 were apparently introduced by man and only 12 are endemic. To illustrate the distance yet to be traveled along the road to fully cataloging biodiversity, five of the 12 endemics are described as new in the work and several unplaceable species are thoroughly covered. There are 187 named species, but the authors state that these are equaled by unnamed species.

The first chapter defines the family and hypothesizes a phylogeny based on several character states. The four subfamilies are also analyzed. The next chapters deal in depth with morphology, including morphology of all early stages in detail and biology. The range of life histories is fascinating as most species are aphytophagous. Before the major section describing the genera in detail there is a brief chapter on diversity and distribution. There are concluding chapters on unplaced species and excluded species and finally comprehensive citations.

This scholastically noteworthy series of publications demands support. Next up is a volume by I. F. B. Common on a section of the Oecophoridae to be followed by a butterfly biology book by R. L. Kitching et al.

FLORISSANT BUTTERFLIES: A GUIDE TO THE FOSSIL AND PRESENT DAY SPECIES OF CENTRAL CALIFORNIA. 1992. T. C. Emmel, M. C, Minno and B. A. Drummond. 118 pp + color plates. Stanford, Palo Alto. $14.95 Softcover, $35.00 Hardbound. 8.5 x 11 inches.

This is a very strange book that comes over as a literary *non sequitur*. Although well designed, produced, and illustrated (the dust jacket is striking) one comes away not being sure what it is all about or for whom it was written. The first part is a review paper of the fossil butterflies of Florissant with a bit about fossil insects in general and the geological history of the earth. These fossils were laid down during the mid Tertiary about 35 million years ago. The climate at that time was apparently subtropical, a conclusion open to interpretation. There also have been major climatic episodes since with vast, intricate, yet highly conjectural movements of the plant communities upon which butterflies, as primary herbivores, directly depend.

The second paper that makes up the book is an annotated checklist of the butterflies of Florissant with all species illustrated in color. The lead-ins include sections on habitat diversity, butterfly diversity, a brief description of general life history, behavior, survival, and taxonomy. Jurassic Park is unquestionably more fun.

BUTTERFLIES AND SKIPPERS OF OHIO. 1992. D. C. Iftner, J. A. Shuey, J. V. Calhoun. College of Biological Sciences, Ohio State University, Columbus, Ohio. $40.00 plus $5.00 postage. Softcover. 212 pp incl. 40 pp color plates. 8.5 x 11 inches.

A bravo book that, in terms of information offered, will be the standard

reference for the state for a long time to come. My negative comments center on the rather poor design, with everything shoved too close together and altogether too narrow margins. For so valuable a scholastic work it is a pity the publisher didn't spend a little time with a book designer. to have given it a touch of class. The familial classification used is largely archaic.

Background information makes this a faunistic work of greater than usual interest. This includes a section on plant communities, which are the biotic aggregations to which primary herbivores, such as butterflies, are adapted. In addition to a vegetation map there are good photographs of all plant communities. There are chapters on history and collectors, education and conservation, plant communities, geology and postglacial biogeography, and methods and terminology. There follows the species listing, with county dot maps for each of the 144 listings, foodplants, phenology, nectar sources, community associations etc. An essential volume for all mid-continental libraries and researchers.

THE OWLET MOTHS OF OHIO. 1992. R. W. Rings, E. H. Metzler, F. J. Arnold, and D. H. Harris. College of Biological Sciences, Ohio State University, Columbus, Ohio. $20.00 plus $3.00 postage. Softcover. 219 pp incl. 8 color plates. 8.5 x 11 inches.

A double bravo book by the Ohio Biological Survey that can be viewed as a model for what we are all supposed to be doing as fast as possible in the face of a rapidly diminishing natural world. With the recent federal announcement of a national biological survey, the Ohio institution for this purpose, the Ohio Biological Survey, has made a most pertinent contribution with this and the above work.

The authors relied on the generosity of many individuals and collections managers to bring the book to the standard that it is. The effort required recording 35,441 specimens to 708 species of Noctuids, classified and named following Hodges (1984). A county map with number of specimens from each depicts a highly non-random database, a commonplace in all wide area sampling pictures. The authors admit that a number of species remain to be collected and include a list of the most probable, complemented by a list of excluded species as misidents and mislabeled specimens.

There is a brief section on identification and an introduction to characters used for this end, including genitalic characters. There is a brief review of developmental biology and another on conservation. There are no diversions into controversial matters of higher classification issues within this large and complex family of moths. Quite proper for a work of this kind.

The centerpiece of the work is the listing of species in an annotated checklist format that includes for each species: MONA checklist and McDunnough checklist number, a reference to where an illustration can be found other than on a plate in the book, an estimate of relative abundance and conservation status, an historical note if applicable, and hosts. There is then a map for each species and a seasonal distribution chart for north and south Ohio.

Following is a list of species that qualify for special attention, in particular those for which this status is unknown. There is then a set of descriptions of special habitats in the state, which are not too numerous, but all sound like places one would want to see. Lastly there is the detailed hostplant listing.

Invaluable, and there is still a great deal to do.

**Briefly Noted:**

PAINTED LADIES: BUTTERFLIES OF NORTH AMERICA. 1993. M. Miller and C Nelson. 64 pp. Johnson Press, Boulder, CO. $5.95. 4 x 6 inch notepad format, all color.

One of those charming hand lettered watercolored general compendia that is actually a tad difficult to read and a bit too cute. The piece carries an amazing amount of information, however, with maps and life histories spattered here and there. Oddly, some species have scientific names while binomials are missing for others. A best buy to get that youngster involved, and the book covers the west as well as the usual east.

PETERSON FIRST GUIDE TO CATERPILLARS. 1993. A. Wright. 128 pp. Houghton, Mifflin. Boston. $4.95. 3.75 x 7.25 inches, soft bound.

"A simplified field guide to the caterpillars of common butterflies and moths of North America." A nice piece for children and casual naturalists that might pique their interest to look beyond the superficial. Strictly eastern U.S. No scientific names. Good price for gift giving.

ANNOTATED LIST OF ONTARIO LEPIDOPTERA. 1992. J.C.E. Riotte. $C19.95. 208 pp. Royal Ontario Museum, Ontario. 6 x 9 inches. softcover.

The content is completely described by the title. The only figures are maps giving political boundaries and depicting faunal regions. Foodplant data are not given. Subspecies names are not used, a pity in the case of the butterflies, while for butterflies the familial supersplitting of earlier mindsets is retained.

FOODPLANTS OF WORLD SATURNIIDAE. 1991. S. E. Stone. 186 pp. Lepidopterists Society, Manhattan Beach, CA. $7.20-$15.00. 16 x 24 cm. softcover.

A compendium of foodplant records for 505 species and subspecies of these large moths. Cross referenced to plant families and species. Many are polyphagous. Unfortunately there is no attempt to analyze patterns of co-adaptation, but here are the data for someone with such interest. Individuals like Stone are to be praised for the enormous labor performed in bringing together basic data as is presented here. The cover is very attractive, but unfortunately the text was run on a laserwriter and not linotronic. In the future this sort of book would be most efficiently handled as a database on diskette.

HANDBOOK FOR BUTTERFLY WATCHERS. 1992. R. M. Pyle. Houghton Mifflin, Boston. 280 pp. $11.95. softcover. 8.25 x 5.5 inches.

One cannot add much to the widespread acclaim Bob Pyle has received for this classic piece, now released in a new printing. He has opened a new view of lepidopterology with a greater population of people beginning to watch butterflies rather than pin them down. The book to buy for anyone interested in these insects. Note the important chapter: "Moths: learning to love them."

THE BUTTERFLY. 1992. M. M. Mudd. Stewart, Tabori & Chang. New York. $12.95. 9 x 12 inch hardcover, pop-up, all color.

Part of a "Dimensional Nature Portfolio" series that include a piece each on the spider, beetle, and bee. The piece is not a book, but a folder from which a giant Monarch butterfly emerges on opening. Several side folders have additional pop-ups and windows. The quality of work is surprisingly good. May be of some value

in schools, but overall my impression is one of too many publishers rushing to fill a popular market that may not have the demand they expect.

BUTTERFLIES OF THE FLORIDA KEYS. 1993. M. Minno and T. C. Emmel. Scientific Publishers. Gainesville. 168 pp. 8.5 x 11 inches

An exhaustive treatment of the butterfly fauna of the Florida Keys including summaries of the history, climate, geology, biogeography, and plant communities. All species illustrated in color, with detailed flight time data given. Conservation biology issues examined, and species-area study presented on distribution among the various islands. Curiously the number of species included, 106, is identical to butterfly species richness of greater Los Angeles.

ATLAS OF WESTERN USA BUTTERFLIES. 1993. R. E. Stanford & P. A. Opler. Published by authors. $17.00 postpaid. 275 pp. spiral bound. 8.5 x 11 inches.

This fine service paper gives a county map of the western US, i.e., those states west of the 100th meridian, with recorded presence of each species distribution presented as four maps per page. An enormous amount of data distilled from many published sources. For the future this information would be best made available as a database format on diskette.

BUTTERFLIES THROUGH BINOCULARS: A FIELD GUIDE TO BUTTER-FLIES IN THE BOSTON, NEW YORK, WASHINGTON REGION. 1993. J. Glassberg. Oxford, New York. $19.95 softcover. $49.95 hardcover. 160 pp + 40 color plates. 8.25 x 5.5 inches.

A popular directed guide to butterfly watching across the dense population corridor of the eastern US. A bargain book for its great deal of well organized information joined with good quality color photographs of most species taken in the field. There is the usual difficulty in discriminating dusky skippers using the illustrative material, but what else is new? An excellent supplement to Pyle's butterfly watchers book for the area covered. It is amazing what a growth industry popular, non-collector oriented books have become. Will the Audubon Society be superseded by a Scudder Society? But then are butterflies becoming more invisible? And will people learn to love moths?

*Rudi Mattoni, Department of Geography, University of California Los Angeles, Los Angeles, CA 90024, USA.*

# INSTRUCTIONS TO AUTHORS

**Manuscript format: Two** copies *must* be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. If possible italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All **measurements** must be metric. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (e.g. 6.IV.1992). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

**Electronic submission**: The Journal is now being produced via desktop publishing, allowing much shorter publication times. Although typewritten manuscripts are acceptable, those submitted on computer disk are *highly* preferred. After being notified of your paper's acceptance, submit either a Macintosh or IBM disk (3.5 inch) version. Include on your disk both the fully formatted copy from your word processing program and a text-only (ASCII) copy. The two most preferred formats are Microsoft Word (Macintosh or IBM) and Word Perfect (IBM), although translation utilities will allow conversion from most formats. Put returns only at the ends of paragraphs, not at the end of each line. Use one tab to indent each paragraph. Even if your printer is incapable of outputting italics, please specify italics rather than underline in your disk copy. Please note in your cover letter any special characters that are used in either the body of the text or the tables (e.g. é, ü, °, §, µ, ♂, ♀).

**Title material:** All papers must include the title, author's name, author's address, and any titular reference and institutional approval reference. A **family citation** *must* be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

**Abstracts and Short Papers:** All papers exceeding three typed pages must be accompanied by an abstract of no more than 300 words. Neither an additional summary nor key words are required, though key words will be included if provided.

**Name citations and Systematic Works:** The first mention of any organism should include the full scientific name with unabbreviated author and year of description. There *must* be conformity to the current International Code of Zoological Nomenclature. We strongly urge depositing of types in major museums, all type depositories must be cited.

**References:** All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations should not be used; write out the entire journal name. Do not underline or italicize periodicals. If four or less references are cited, please cite in body of text not in Literature Cited. For multiple citations by the same author(s), use six hyphens rather than repeating the author's name.

**Tables:** When formulating tables, keep in mind that the final table will fill a maximum space of 11.5 by 19 cm either horizontally or vertically oriented. Number tables with Arabic numerals. When submitting tables on disk, use tabs between columns rather than multiple spaces.

**Illustrations:** Color can be submitted as either a transparency or print, the quality of which is critical. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors *must* plan on illustrations for reduction to page size. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink. Include a metric scale. Each figure should be cited and explained as such. Each illustration must be identified by author and title on the back. Indicate whether you want the illustration returned at your expense. Retain original illustrations until paper is accepted. **Legends** should be separately typed on pages entitled "Explanation of Figures." Number legends consecutively with separate paragraph for each page of illustration.

**Review:** All papers will be read by the editor(s) & submitted for formal review to two referees.

**IN THIS ISSUE**

COVER ILLUSTRATION: Above: 5th instar *Ancyluris inca*, a common second growth non-myrmecophilous species. Below: 5th instar *Nymphidium mantus* drinking at an extrafloral nectary of its hostplant. Note the *Azteca* sp. (Dolichoderiinae) ant drinking from the tentacle nectary organs. Drawings by Jennifer Clark from slides by Phil DeVries for upcoming fieldguide to riodinid butterflies of Costa Rica.

# The Journal of Research on the Lepidoptera

*Fall 1992*

# THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

---

# Exploitation of lycaenid-ant mutualisms by braconid parasitoids

Konrad Fiedler[1], Peter Seufert[1], Naomi E. Pierce[2], John G. Pearson[3] and Hans-Thomas Baumgarten[1]

[1] Theodor-Boveri-Zentrum für Biowissenschaften, Lehrstuhl Zoologie II, Universität Würzburg, Am Hubland, D-97074 Würzburg, Germany
[2] Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138-2902, USA
[3] Division of Natural Sciences and Mathematics, Western State College, Gunnison, CO 81230, USA

**Abstract.** Larvae of 17 Lycaenidae butterfly species from Europe, North America, South East Asia and Australia were observed to retain at least some of their adaptations related to myrmecophily even after parasitic braconid larvae have emerged from them. The myrmecophilous glandular organs and vibratory muscles of such larval carcasses remain functional for up to 8 days. The cuticle of lycaenid larvae contains extractable "adoption substances" which elicit antennal drumming in their tending ants. These adoption substances, as well, appear to persist in a functional state beyond parasitoid emergence, and the larval carcasses are hence tended much like healthy caterpillars. In all examples, the braconids may receive selective advantages through myrmecophily of their host larvae, instead of being suppressed by the ant guard. Interactions where parasitoids exploit the ant-mutualism of their lycaenid hosts have as yet been recorded only from the *Apanteles* group in the Braconidae-Microgasterinae.

**KEY WORDS:** Lycaenidae, Formicidae, myrmecophily, adoption substances, parasitoids, Braconidae, *Apanteles*, defensive mechanisms

## INTRODUCTION

Parasitoid wasps or flies are major enemies of the early stages of most Lepidoptera (Shaw 1990, Weseloh 1993). The mostly endophagous larvae of the wasp family Braconidae usually develop in caterpillars of various Lepidoptera or, more rarely, in the larvae of certain Hymenoptera or Diptera. Larvae of Microgasterinae braconids are either solitary or gregarious parasitoids, depending on the species (Papp 1990, Shaw 1990). In this economically important subfamily, the parasitoid larvae leave their hosts and pupate externally in a silken cocoon. This cocoon may either be attached to the host's carcass, as in the case of the well-known *Cotesia glomerata* (L.) parasitizing the cabbage white, *Pieris brassicae* (L.), or to the hostplant. With very few exceptions (e.g. Brodeur and Vet 1994), a host caterpillar will die soon after Microgasterinae larvae have emerged.

Lepidopterous caterpillars have evolved a variety of strategies to escape parasitoid attacks. One peculiar strategy is found among myrmecophilous members of the butterfly families Lycaenidae and Riodinidae. These larvae attract ants with the help of specialized exocrine glands (Malicky 1969, Pierce 1983, Cottrell 1984). Larval secretions contain carbohydrates and amino acids which serve as additional nutrition for tending ants (Maschwitz et al. 1975, Pierce 1983, Fiedler & Maschwitz 1988a). In turn, the ants may effectively protect the caterpillars against certain enemies, including parasitoids (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987, Seufert & Fiedler 1994). Such butterfly-ant interactions then represent true mutualisms, analogous to the well-known trophobiotic associations between honeydew-producing Homoptera and ants.

At least three types of myrmecophilous glands are important in lycaenid-ant interactions. The dorsal nectar organ (located mediodorsally on the 7th abdominal segment, DNO hereafter) secretes droplets of a nutrient-rich fluid when stimulated through antennation by ants (Malicky 1969, Cottrell 1984). In addition, many Lycaenidae caterpillars possess a pair of eversible tentacle organs (TOs hereafter) on the 8th abdominal segment. These organs are mostly everted when the caterpillars are disturbed, or while moving to feeding or resting places. Ants respond with a state of alert to TO eversions, apparently mediated through volatile chemicals (Henning 1983, Fiedler & Maschwitz 1988b, Ballmer & Pratt 1992). A third type of myrmecophilous organs are the pore cupolas (PCOs), minute hair-derived epidermal glands whose secretions are often highly attractive to ants (Malicky 1969, Pierce 1983). PCOs are generally found in larvae as well as pupae of lycaenid butterflies, even if stable symbiotic associations with ants do not occur. Finally, so-called dendritic setae appear to be related to caterpillar-ant interactions, since the locations of these setae in larvae or pupae generally receive the greatest attention of visiting ants (Ballmer & Pratt 1992, Fiedler, pers. observ.).

In addition, immatures of many Lycaenidae species produce substrate-borne vibrations (DeVries 1991a). In analogy to the "calls" of certain myrmecophilous Riodinidae (DeVries 1990), vibrations of Lycaenidae larvae may enhance their symbioses with ants, although the occurrence of substrate-borne vibrations in certain non-myrmecophilous lycaenid species suggests that vibratory behavior is not exclusively connected with myrmecophily and may serve another function (possibly defense) in these species (Schurian & Fiedler 1991, Fiedler 1992a, 1994; see also Downey & Allyn 1978 for pupal sounds).

Behavioral interactions between lycaenid caterpillars, their parasitoids and attendant ants have as yet received little attention, although the protective role of tending ants against parasitoids has been established in a few lycaenid species (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987). Pierce et al. (1987) and Nash (1989) obtained evidence that a specialist parasitoid of the Australian obligate myrmecophile *Jalmenus evagoras* Domovan may use attendant *Iridomyrmex*

*anceps* ants as host-location cues. Recently, Schurian et al. (1993) described how adult braconid wasps utilize ant-related secretions of their host caterpillars. In this paper, we investigate two additional aspects of such multi-species interactions. First, we use a simple behavioral bioassay to investigate the chemical nature of "ant adoption" substances secreted by larvae of the Nearctic species, *Glaucopsyche lygdamus* Doubleday. Second, we document that particular species of parasitoids consume their lycaenid hosts in ways that take advantage of the myrmecophilous properties of the caterpillars. We here summarize our findings on 17 butterfly species, representing 13 genera in 2 subfamilies.

## MATERIALS AND METHODS
### Adoption substances in *Glaucopsyche lygdamus* larvae

100 final instar caterpillars of the Nearctic *G. lygdamus* were sampled at Gothic, Colorado (elevation 2900 m), in July 1980 and stored frozen at -20 °C. From these larvae, two groups of tissue preparations were made, viz. "dorsal epidermis" and "ventral epidermis". PCOs as well as other setae which may play a role in ant-caterpillar interactions (e.g. dendritic setae: Ballmer & Pratt 1992) are too small to permit individual excision, but morphological analyses revealed that these structures are common dorsally, but rare (PCOs) or absent (dendritic setae) on the ventral side of the caterpillars (e.g. Ballmer & Pratt 1989). Wet tissue samples (208 mg dorsal epidermis and 20 mg ventral epidermis) were weighed and extracted with 50 µl of solvent per mg of tissue. This approach equalizes concentrations of ions or extractable substances between experimental (dorsal) and control (ventral) tissues. Extraction was accomplished by grinding tissue samples in glass vials with flanged glass rods. Redistilled dichloromethane was used as solvent.

Pre-packaged silica gel thin-layer plates (EM, 25 µ) were spotted with 100 µl of tissue extract (dorsal, ventral) or solvent. On some plates cholesterol was also spotted as a standard indicator. Before solvent development, spotted material was first assayed for biological activity with a tissue paper overlay protecting the plates. Plates were then developed at 4 °C with hexane/ethyl-acetate/ethanol (92:6:2), and as soon as these plates had dried, the bioassay was carried out with a tissue paper overlay marked in 1 cm bands for each sample. Following bioassay, separated components were visualized by iodine vapor. Eight trials were conducted.

Queenright colonies of *Formica altipetens*, kept in artificial nests and fed on a diet of honey water and freshly killed insects with access to ad libitum water, were used for bioassays. Treated TLC plates were offered at a distance of 10 cm from the entrance to the ant nest in a foraging arena (71 × 142 cm) in which an ant colony was placed. Behavioral responses of the ants were scored as a percentage of the number of times that workers stopped and drummed over the total number of encounters during a 15 min period.

### Interactions between ants and parasitized caterpillars or larval carcasses

During our studies on the life-cycles of various Lycaenidae species in Central Europe, North America, South East Asia and Australia, we repeatedly collected caterpillars that later turned out to be parasitized. Field-collected caterpillars

of 17 species (Table 1) were reared in the laboratory together with their
attendant ants, until parasitoids left their host caterpillars to pupate. Some
individuals were left under natural conditions on their hostplants. Behaviors of
ants before and after parasitoid emergence were noted, and the activity of the
myrmecophilous organs of the caterpillars as well as their ability to produce
substrate-borne vibratory signals were followed until the carcasses eventually
lost attractiveness to ants. Vibrations were monitored using a stethoscope
(Schurian & Fiedler 1991).

## RESULTS

### Adoption substances in the epidermis of *Glaucopsyche lygdamus*

Whenever worker ants tend lycaenid larvae in nature, a characteristic
antennal drumming is one main component of ant-caterpillar interac-
tions (Malicky 1969, 1970). We used this behavioral trait as an indicator
of ant response to lycaenid adoption substances: immediately upon
encountering a spot of dorsal skin extract, a *F. altipetens* worker would
often drum on the spot in exactly the same manner as she would on a
caterpillar in the field. Workers never recruited nestmates to the spots,
and tactile stimulation appeared to be necessary to elicit ant response
as workers did not move preferentially upwind toward fresh caterpillars
when air was passed over them in a Y-tube olfactometer (Pierce,
unpubl.).

Workers investigated the extract of dorsal skin significantly more
often than the extract of ventral skin (i.e. "controls"). With dorsal
extracts, $57.0 \pm 17.7$ % (mean $\pm$ S.D.) of all encounters resulted in
drumming responses, whereas with ventral extracts the average figure
was $30.6 \pm 17.6$ % (8 paired trials, $p < 0.005$, Wilcoxon signed-ranks test).
Although myrmecophilous organs are almost absent from the ventral
surface of a caterpillar, the ventral control extracts still contained low
activity. We attribute this to the unavoidable crudeness of the tissue
preparation. Fig. 1 presents the data compiled from developed TLC
plates. Nine spots were found on each chromatogram for both the dorsal
and ventral extracts. These correspond to $R_f$ values of 0.15, 0.18, 0.33,
0.43, 0.45, 0.49, 0.53, 0.54, and 0.96. For each trial, the mobilities and
spot sizes were identical between the two samples, while the solvent
control did not afford any visualizable material nor did it receive
antennation by ants.

The most active band on the TLC ($R_f = 0.96$, section 12) appears near
the solvent front. Together with extraction by methylene chloride, this
mobility suggests a substance of low polarity. In addition, since the
substance remains on TLC plates after initial bioassay, plate develop-
ment, solvent evaporation and final bioassay, it would seem to be of low
volatility. Although we did not quantify this effect, the activity of the
substance appeared to decrease with time, suggesting that it eventually
evaporates or undergoes chemical alteration on TLC plates. The activity
around position 3.5 corresponds to an $R_f$ value of about 0.43, coinciding
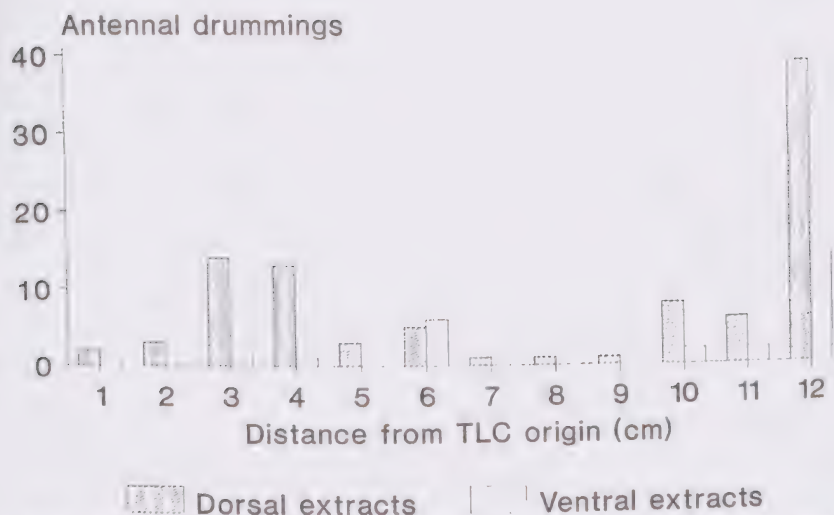
**Antennal drummings**



Fig. 1. Total number of antennal drumming responses of *Formica altipetens* worker ants towards separated compounds of epidermal extracts of *Glaucopsyche lygdamus* caterpillars on developed TLC plates. Given are cumulative numbers over a total test period of 120 min. A compound which occurred in section 12 elicited the greatest response and corresponded to an $R_f$ value of 0.96. A compound which occurred inbetween fractions 3 and 4 showed some activity and corresponded to an $R_f$ value of 0.43.

with the respective value of cholesterol. We have no evidence whether the ants are attracted to cholesterol or another compound at that position.

## Persistence of myrmecophily in parasitized caterpillars or larval carcasses

In most cases, a parasitized lycaenid caterpillar would die, or has already been killed, when its parasitoid larvae are ready to pupate. This was invariably the case with caterpillars parasitized by Tachinidae flies (observations with following lycaenid species: *Jalmenus evagoras*, *Thecla betulae*, *Arhopala amphimuta*, *Drupadia theda*, *Hypolycaena erylus*, *Rapala dieneces*, *Callophrys rubi*, *Jamides malaccanus*, *J. caeruleus*, *Glaucopsyche alexis*, *G. lygdamus*, *Polyommatus coridon*, *P. icarus*), and with certain ichneumonids (*Hyposoter*, Campopleginae) or braconids (*Aleiodes*, Rogadinae), which pupate inside the host cuticle (e.g. in *Drupadia ravindra*, *Scolitantides orion*, *Aricia eumedon*, *Polyommatus coridon*; Fiedler, pers. observ.). However, when caterpillars are parasitized by members of the *Apanteles* group (Braconidae-Microgasterinae), the larvae often remain attractive to their tending ants and the myrmecophilous organs may stay functional for several days beyond parasitoid emergence. The following observations were made (categorized by the

Table 1. Summary of observations on the function of myrmecophilous organs and the persistence of vibratory abilities in parasitized caterpillars of 17 Lycaenidae butterfly species. Only observations involving parasitoids of the braconid subfamily Microgasterinae are considered. [1]: DNO intensively antennated, but secretion act not observed. [2]: not recorded. [3]: species with non-functional rudimentary DNO. Facultative myrmecophiles associate with a variety of ant taxa, but are not dependent on ant-attendance. Obligate myrmecophiles invariably live in symbiosis with a specific host ant. A (g) or (s) behind the parasitoid's name indicates gregarious (multiple wasps per host) or solitary parasitoids. The 4 parasitoids from the *Apanteles ater*-group represent different species.

| Butterfly species | Interaction with ants | DNO | TOs | Vibrations | Attractive to ants | Parasitoid |
| --- | --- | --- | --- | --- | --- | --- |
| | | —— function persisting —— | | | | |
| *Curetis* sp. (n = 3) | not myrmecophilous | absent | 3-4 d | 3-4 d | no | *Apanteles* nr. *ater* (g) |
| *Jalmenus evagoras* | obligate myrmecophile | ?² | ?² | ?² | yes | *Apanteles* sp.(s) |
| *Surendra florimel* (n = 6) | facultative myrmecophile | ?¹ | > 4 d | 4-7 d | yes | *Apanteles* nr. *ater* (s) |
| *Drupadia theda* (n = 17) | obligate myrmecophile | ?¹ | 4-7 d | 3-8 d | yes | *Apanteles* nr. *prosymna* (g) |
| *Cheritra freja* (n = 2) | not myrmecophilous | absent | absent | no | no | *Apanteles* nr. *prosymna* (g) |
| *Hypolycaena othona* (n = 1) | facultative myrmecophile | no | absent | 6 d | yes | *Apanteles* sp. (s) |
| *H. erylus* | obligate myrmecophile | ?² | ?² | ?² | yes | *Apanteles* sp. |
| *Callophrys rubi* (n = 10) | not myrmecophilous | absent³ | absent | > 2 d | no | *Distatrix sancus* (g) |
| *Anthene emolus* (n = 14) | obligate myrmecophile | 1-3 d | no | 2-5 d | yes | *Apanteles* nr. *ater* (s) |

| | | | | | | |
|---|---|---|---|---|---|---|
| Jamides malaccanus (n = 4) | facultative myrmecophile | ?[1] | 1 d | no | yes | Apanteles nr. ater (s) |
| Caleta manovus (n = 1) | not myrmecophilous | absent | absent | 1 d | no | Apanteles sp. (s) |
| Glaucopsyche alexis (n = 1) | facultative myrmecophile | ?[2] | ?[2] | > 2 d | ?[2] | Cotesia cupreus (g) |
| G. lygdamus (n = 4) | facultative myrmecophile | ?.2 | ?.2 | ?.2 | yes | Apanteles cyaniridis (g) |
| Plebejus melissa (n = 1) | facultative myrmecophile | ?.2 | ?.2 | ?.2 | yes | Apanteles sp. (g) |
| Polyommatus coridon (n = 3) | facultative myrmecophile | ?[1] | 2 d | 2-3 d | yes | Cotesia cupreus (g) |
| P. coridon (n = 60) | facultative myrmecophile | no | no | no | yes | Cotesia saltatoria (s) |
| P. bellargus (n = 1) | facultative myrmecophile | 6 d | 6 d | 6 d | yes | Cotesia cupreus (g) |
| P. icarus (n = 1) | facultative myrmecophile | 5 d | 6 d | 5 d | yes | Cotesia cupreus (g) |

myrmecophilous organs, respectively; see Table 1 for synopsis of observations):

### THE DORSAL NECTAR ORGAN (DNO) REMAINS ACTIVE IN PARASITIZED CATERPILLARS

*Anthene emolus*, a widespread Oriental lycaenid butterfly, is an obligatory myrmecophile which is specifically associated with the aggressive weaver ant, *Oecophylla smaragdina*. Caterpillars of *A. emolus* secrete droplets from the DNO at particularly high rates (200-300 droplets/h: Fiedler & Maschwitz 1989). In April and May 1993, we found a total of 14 parasitized individuals (infested by a solitary parasitoid species of the *Apanteles ater* group) at Ulu Gombak (West Malaysia), on the hostplant tree *Saraca thaipingensis* (Caesalpiniaceae). From 6 caterpillars, the wasp larva had already emerged and pupated at the time of collection. Each of these caterpillars sat motionless on the silken braconid cocoon attached to its ventral side. The remaining 8 caterpillars were collected as second to early fourth (= final) instars while feeding, and the braconid larvae emerged later in captivity.

In both the field and the laboratory, all 14 caterpillars remained fully attractive to their specific host ant even after the parasitoids had emerged. One or two *Oe. smaragdina* workers constantly attended and antennated each larval "carcass". These responded with regular eversions of the DNO, and the secretion droplets were frequently visible (Fig. 2). *Oe. smaragdina* ants eagerly harvested every single droplet. The ability to deliver DNO secretions persisted in *A. emolus* caterpillars up to 3 days after the braconid larva had emerged. Attractiveness of the caterpillar carcasses to *Oecophylla* ants persisted 4-5 days, and the adult braconids eclosed after a pupal period of 5-6 days. In *A. emolus*, eversions of the TOs were not seen after parasitoid emergence.

DNO secretions after parasitoid emergence could as yet be ascertained in two additional Lycaenidae species, the Palearctic facultative myrmecophiles *Polyommatus bellargus* and *P. icarus*. One mature *P. bellargus* caterpillar (origin near Würzburg, northern Bavaria), from which 24 *Apanteles* larvae had emerged and pupated at the ventral side, secreted droplets from the DNO up to the sixth day beyond parasite emergence. This caterpillar was caged with *Lasius flavus* ants for only 1-5 minutes

Fig. 2. *Oecophylla smaragdina* worker ants drink a secretion droplet from the dorsal nectar organ of a parasitized *Anthene emolus* caterpillar (Ulu Gombak, West Malaysia). The white *Apanteles* cocoon is attached to the ventral side of the host. Photograph P. Seufert.

Fig. 3. A fourth instar caterpillar of *Curetis* sp. (Ulu Gombak, West Malaysia) with everted tentacle organs after tactile disturbance. Note the dense pillow of *Apanteles* cocoons on the ventral side. Photograph P. Seufert.

Fig. 4. Parasitized carcass of mature caterpillar of *Polyommatus icarus*, offering a nectar droplet to tending *Lasius flavus* ants the day after parasitoid emergence. Photograph K. Fiedler.

per day to prevent the rapid depletion of the DNO reservoir content. By
this procedure, 21 DNO secretion droplets were observed in a total
observation period of 7.5 minutes spread over 4 days. Using the same
test procedure with the same ant species, a mature *P. icarus* caterpillar
(origin near Würzburg, northern Bavaria) from which 14 braconid
larvae had emerged, delivered 12 DNO secretion droplets in 8 minutes
total observation period spread over 5 days (Fig. 4).

We observed antennation at, and eversion of, the DNO in larvae of 4
additional species (Table 1) which were kept together continuosly with
attendant ants. *S. florimel*, *J. malaccanus*, and *P. coridon* are faculta-
tive myrmecophiles whose mature caterpillars are tended by a variety
of ant taxa (Fiedler 1991, 1992b and unpubl.), while *D. theda* is
obligatorily connected with certain *Crematogaster* species (Maschwitz
et al. 1985; Seufert & Fiedler 1994). We suppose that secretions occurred
even after parasitoid emergence in these cases, but that the gland
reservoirs of the caterpillars had been depleted at the time of observa-
tion due to continuous milking by ants.

THE TENTACLE ORGANS (TO) REMAIN ACTIVE IN CATERPILLAR CARCASSES

The TOs of 6 myrmecophilous Lycaenidae species (Table 1) remained
fully active for up to 7 d beyond braconid emergence and still elicited the
typical behavioral reaction (alert, "excited runs": Fiedler & Maschwitz
1988b) in their tending ants. TO eversions occurred in the following
pairs of interacting species: *S. florimel* with *Rhoptromyrmex wroughtonii*
(Myrmicinae), *Technomyrmex* and *Iridomyrmex* sp. (Dolichoderinae);
*D. theda* with *Crematogaster* sp. (Myrmicinae); *J. malaccanus* with
*Camponotus* (subgenus *Tanaemyrmex*) sp. (Formicinae) and
*Crematogaster*; and the 3 *Polyommatus* species with *Lasius flavus*
(Formicinae).

Caterpillars of the Oriental genus *Curetis* (subfamily Curetinae: Eliot
1990) have highly modified and very large TOs situated in elevated
epidermal cylinders. The TOs are thrusted rapidly after tactile distur-
bance of a caterpillar, making visible the long, conspicuous, black-and
white hairs (DeVries et al. 1986; Fiedler et al. 1995). This striking
defensive behavior continued in three parasitized *Curetis* caterpillars
found at Ulu Gombak in May 1993 for 3-4 d after emergence and
pupation of the larvae of a gregarious braconid species (*Apanteles ater*
group; Fig. 3). A specific identification of the host butterfly is impossible,
because the parasitized larvae have been collected on the same hostplant
tree (*Millettia atropurpurea*, Fabaceae) together with early stages of
*Curetis bulis* and *C. santana*, whose larvae look almost identical. *Curetis*
caterpillars are rarely, if ever tended by ants (DeVries 1984; Fiedler et
al. 1995).

LARVAL CARCASSES REMAIN ATTRACTIVE TO THEIR TENDING ANTS

Larval carcasses of 12 species (Table 1) were persistently, or at least
temporarily, tended by ants for up to 5 d beyond parasitoid emergence.

Such interactions were observed in the field as well as in captivity, involving ants of the genera *Crematogaster, Rhoptromyrmex, Lasius, Formica, Camponotus, Oecophylla, Dolichoderus, Technomyrmex* and *Iridomyrmex*. These ants showed the same antennal drumming towards healthy caterpillars, and antennation was not restricted to the DNO nor to the vicinity of the TOs.

PERSISTENCE OF VIBRATORY BEHAVIOR

The ability to produce substrate-borne vibrations persisted in 11 lycaenid caterpillar species including three non-myrmecophiles (Table 1), sometimes up to 8 d beyond parasitoid emergence. Except in *Cheritra freja*, there was no indication that the vibratory behavior of parasitized caterpillars, and later carcasses, differed in any respect from that of healthy caterpillars. Vibratory behavior was most easily elicited by tactile disturbance of the larvae (e.g. handling with forceps). *Ch. freja* is a myrmecoxenous member of the hairstreak subtribe Cheritriti. In this species, even healthy larvae only occasionally made vibratory calls after tactile disturbance (2 out of 15 in our sample), and in two fourth (= final) instars, which were parasitized by a gregarious *Apanteles* species (nr. *prosymna*), calls were recognized neither before nor after parasitoid emergence.

DISCUSSION

Observations on behavioral interactions between lycaenid caterpillars and their parasitoids are typically chance findings. Experimental work with larger sample sizes is prohibited by the scarcity or crypsis of both hosts and parasitoids. Moreover, the taxonomy of the parasitoids involved is still in a very incomplete stage, especially in the tropics, and information on host ranges or specificity is almost unavailable. Hence, the observations and conclusions presented here are by necessity based on small numbers of sometimes anecdotal observations. Nevertheless, collectively these provide circumstantial evidence that certain parasitoids may take advantage of the mutualistic relationships between their lycaenid host larvae and ants.

Breaking the chemical communication code between lycaenids and ants is an essential facet of parasitoid subterfuge. Besides delivery of nutritive secretions (such as those derived from the DNO), lycaenid caterpillars possess extractable components in their integument which serve as "adoption substances". These epidermal substances induce non-aggressive antennal drumming in the ants when tending lycaenid immatures. Although their chemical composition remains unknown, these substances are of low volatility. Physical contact is necessary to induce caterpillar-ant interactions. The adoption substances retain biological activity for some time, as shown in the experiments with extracts. Furthermore, caterpillar carcasses left by braconid parasitoids, and occasionally even empty pupal cases, remain attractive to

tending ants for hours or days. This strongly suggests that the adoption substances remain functional. The PCOs, ubiquitous glandular structures of lycaenid immatures, are likely to be one source of these adoption signals, although the significance of other organs, such as dendritic setae, remains to be addressed.

In *Anthene emolus*, *Polyommatus bellargus*, *P. icarus*, and probably in four additional species where ants antennated the DNO of the larval carcasses, even the ability to secrete droplets from the DNO persisted, although this property typically ceased first. This may be explained by depletion of the secretion supply in the glandular reservoir. After feeding has stopped, caterpillars cannot replenish their secretion stock. The 12 DNO secretion droplets observed in *P. icarus* after parasitoid emergence, and the 21 droplets in the case of *P. bellargus*, closely match the estimated DNO reservoir content in these species. Using Malicky's (1969) histological data, the total reservoir volume is roughly 0.06 µl in *P. icarus*, which corresponds to c. 15 droplets with an average volume of 0.004 µl (Fiedler & Burghardt, unpubl.). For *P. bellargus*, the respective figure is a DNO volume of 0.131 µl corresponding to 22 droplets of 0.006 µl averge size (based on histological and experimental data from the closely related *P. coridon*).

Vibratory abilities and TO activity persisted longer than DNO secretions. Both these behaviors are executed by specialized muscles. In addition, limited capacities to move persisted in the Lycaenidae species listed in Table 1. From these observations we conclude that part of the peripheral musculature (i.e. those muscles necessary for DNO and TO activity, or for producing vibratory calls) is exempted from exploitation by these Microgasterine parasitoids. With the exception of *Anthene emolus*, whose parasitized caterpillars reached only half the size of healthy larvae, the larvae listed in Table 1 did not show retarded growth and attained normal size despite parasitoid infestation.

Sparing of myrmecophilous properties occurred in solitary as well as gregarious species, but all records yet available of such phenomena are from the *Apanteles* group in the braconid subfamily Microgasterinae. We have so far never observed comparable interactions in lycaenid caterpillars parasitized by various species of Tachinidae flies, Ichneumonidae wasps, or braconids from other subfamilies (e.g. Rogadinae). Even among the Microgasterinae, this trait is not universal. *Cotesia saltatoria*, for example, is a solitary parasitoid that emerges when the host caterpillars are still rather small (third instar). In this case, the host soon dies after parasitoid emergence, and neither activity of the myrmecophilous organs nor vibratory behavior could be observed, although the carcasses remained attractive to *Lasius flavus* ants for up to 3 d.

Parasitoids of lepidopterous caterpillars greatly vary in the extent of damage they impose on their hosts. All tachinid flies which we have reared so far from Lycaenidae caterpillars leave only a limp cuticle and

Fig. 5. Larvae of *Apanteles cyaniridis*, freshly emerged from mature *Glaucopsyche lygdamus* caterpillar. The wasp larvae are not attacked by the attendant ant (*Formica* sp.). Photograph N. E. Pierce.

entirely consume all internal host tissues (observations made on a number of Lycaenidae species, see above), and neither secretory nor vibratory abilities persisted. Instead, the caterpillars were abandoned by their tending ants 1-2 days prior to parasitoid emergence and vibratory behavior likewise ceased at roughly that time.

If sparing of myrmecophilous properties of Lycaenidae hosts should turn out to be a specific adaptation of certain Microgasterinae braconids rather than an accidental or commonplace epiphenomenon, what selective advantage may these parasitoids derive from this behavior? Although experimental evidence has not yet been obtained, it is likely that the wasps benefit in at least three ways. First, their pupal cocoons are covered by their well-camouflaged hosts and may thereby escape visually searching predators or hyperparasitoids. In all the species listed in Table 1, except sometimes in *Cotesia saltatoria*, the cocoons are tightly attached to the caterpillar. The gregarious species often formed well-defined pillows of cocoons, on which the host carcass sat motionless for days (Fig. 3).

Second, the potentially vulnerable larvae of braconids emerging from the carcasses of their lycaenid hosts somehow avoid attacks by ants which attend the lycaenids. Larvae of *Apanteles cyaniridis* emerging

from *Glaucopsyche lygdamus*, for example, were observed to be inspected by attendant ants, but not attacked (Fig. 5; also Fiedler 1992b). Within a few minutes after emergence from their hosts, these parasitoid larvae spin protective cocoons and pupate beneath the host's carcass. The mechanism for this striking tolerance remains unknown (see DeVries' (1991b) discussion of appeasement versus ignorance).

Finally, by sparing the myrmecophilous properties of their hosts, these braconids are indirectly attended by ants for at least the first part of their own pupal development. Recent work on aphidiid parasitoids of ant-tended aphids has confirmed that certain parasitoids, rather than their host aphids, may benefit from ant-association (Völkl 1992). The interactions between ants, lycaenid caterpillars and Microgasterinae braconids obviously bear a similar potential. In all cases observed so far, the attractiveness of the larval carcasses ceased before the wasps emerged from their cocoons, allowing the wasps to eclose and fly off in the absence of ants.

Together with the apparent use of tending ants as host-location cues by an Australian *Apanteles* species parasitizing *Jalmenus evagoras* (Pierce et al. 1987, Nash 1989), and with the ability of several Microgasterinae wasp species to feed on the secretions which their hosts provide from the myrmecophilous glands (Schurian et al. 1993), our observations indicate that interactions between ants, lycaenid larvae and their braconid parasitoids are even more complex than previously thought.

## LITERATURE CITED

BALLMER, G. R. & PRATT, G. F. 1989. A survey of the last instar larvae of the Lycaenidae of California. J. Res. Lepid. 27:1-81.
———. 1992. Quantification of ant attendance (myrmecophily) of lycaenid larvae. J. Res. Lepid. 30:95-112.
COTTRELL, C. B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zool. J. Linn. Soc. 79: 1-57.
BRODEUR, J. & VET, L. E. M. 1994. Usurpation of host behaviour by a parasitic wasp. Anim. Behav. 48:187-192.

DeVries, P. J. 1984 Of crazy-ants and Curetinae: are *Curetis* butterflies tended by ants? Zool. J. Linn. Soc. 79:59-66.

——. 1990. Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. Science 248:1104-1106.

——. 1991a. Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. Amer. Mus. Novit. 3025:1-23.

——. 1991b. Mutualism between *Thisbe irenea* butterflies and ants, and the role of ant ecology in the evolution of larval-ant associations. Biol. J. Linn. Soc. 43:179-195.

DeVries, P. J., Harvey, D. J. & Kitching, I. J. 1986. The ant associated epidermal organs on the larva of the lycaenid butterfly *Curetis regula* Evans. J. Nat. Hist. 20:621-633.

Downey, J. C. & Allyn, A. C. 1978. Sounds produced in pupae of Lycaenidae. Bull. Allyn Mus. 48:1-14.

Eliot, J. N. 1990. Notes on the genus *Curetis* Hübner (Lepidoptera, Lycaenidae). Tyô to Ga 41:201-225.

Fiedler, K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner zool. Monogr. 31:1-210.

——. 1992a. Notes on the biology of *Hypolycaena othona* (Lepidoptera: Lycaenidae) in West Malaysia. Nachr. entomol. Ver. Apollo Frankfurt N. F. 13:65-92.

——. 1992b. The life-history of *Surendra florimel* Doherty 1889 (Lepidoptera: Lycaenidae) in West Malaysia. Nachr. entomol. Ver. Apollo Frankfurt N. F. 13:107-135.

——. 1994. The life-history of *Caleta roxus* (Lepidoptera: Lycaenidae). Nachr. entomol. Ver. Apollo Frankfurt N. F. 14:371-384.

Fiedler, K. & U. Maschwitz. 1988a. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). II. Lycaenid larvae as trophobiotic partners of ants - a quantitative approach. Oecologia 75:204-206.

——. 1988b. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). III. New aspects of the function of the retractile tentacular organs of lycaenid larvae. Zool. Beitr. Berlin N.F. 31:409-416.

——. 1989. The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. J. nat. Hist. 23:833-846.

Fiedler, K., Seufert, P., Maschwitz, U., & Azarae, I. 1995. Notes on larval biology and pupal morphology of Malaysian *Curetis* butterflies (Lepidoptera: Lycaenidae). Tyô to Ga 45:287-299.

Henning, S. F. 1983. Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). J. Entomol. Soc. Sth. Afr. 46:341-366.

Malicky, H. 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). Tijdschr. Entomol. 112:213-298.

——. 1970. New aspects on the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). J. Lepid. Soc. 24:190-202.

MASCHWITZ, U., SCHROTH, M., HANEL, H. & THO Y. P. 1985. Aspects of the larval biology of myrmecophilous lycaenids from West Malaysia. Nachr. entomol. Ver. Apollo Frankfurt, N. F. 6:181-200.

MASCHWITZ, U., WÜST, M. & SCHURIAN, K. 1975. Bläulingsraupen als Zuckerlieferanten für Ameisen. Oecologia 18:17-21.

NASH, D. R. 1989. Cost-benefit analysis of a mutualism between lycaenid butterflies and ants. Ph. D. thesis, Oxford Univ.

PAPP, J. 1990. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae) XII. Supplement to the key of the *glomeratus*-group. Parasitoid/host list 2. Ann. Hist.-Nat. Mus. Natl. Hung. 81:159-203.

PIERCE, N. E. 1983. The ecology and evolution of symbioses between lycaenid butterflies and ants. PhD Diss., Harvard Univ.

PIERCE, N. E. & EASTEAL, S. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. J. Anim. Ecol. 55:451-462.

PIERCE, N. E. & MEAD, P. S. 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. Science 112:1185-1187.

PIERCE, N. E., KITCHING, R. L., BUCKLEY, R. C., TAYLOR, M. F. J. & BENBOW, K. F. 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. Behav. Ecol. Sociobiol. 21:237-248.

SCHURIAN, K. G. & FIEDLER, K. 1991. Einfache Methoden zur Schallwahrnehmung bei Bläulings-Larven (Lepidoptera: Lycaenidae). Entomol. Z. 101:393-398.

SCHURIAN, K. G., FIEDLER, K. & MASCHWITZ, U. 1993. Parasitoids exploit secretions of myrmecophilous lycaenid butterfly caterpillars (Lycaenidae). J. Lepid. Soc. 47:150-154.

SEUFERT, P. & FIEDLER, K. 1994. *Drupadia ravindra* and *D. theda* (Lepidoptera: Lycaenidae): contrasting systems of myrmecophily among two closely related butterfly species. In: A. Lenoir, G. Arnold & M. Lepage (eds.) Les insectes sociaux, p. 275. Publ. Univ. Paris Nord, Paris.

SHAW, M. R. 1990. Parasitoids of European butterflies and their study. In: O. Kudrna (ed.) Butterflies of Europe, vol. 2, pp. 449-479. Aula Verlag Wiesbaden.

VÖLKL, W. 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? J. Anim. Ecol. 61:273-281.

WESELOH, R. M. 1993. Potential effects of parasitoids on the evolution of caterpillar foraging behavior. In: N. E. Stamp & T. M. Casey (eds.) Caterpillars. Ecological and evolutionary constraints on foraging, pp. 203-223. Chapman & Hall, New York/London.

# Life History of *Attacus mcmulleni* (Saturniidae) from the Andaman Islands, India

K. Veenakumari and Prashanth Mohanraj

Central Agricultural Research Institute, P.B. No. 181, Port Blair-744 101, Andaman & Nicobar Islands, India

and

Richard S. Peigler

Department of Zoology, Denver Museum of Natural History, 2001 Colorado Blvd., Denver, Colorado 80205-5798 U.S.A.

**Abstract.** The life cycle of *Attacus mcmulleni*, a wild silkmoth endemic to the Andaman Islands (India) in the Bay of Bengal, and its immature stages are described and figured. Comparisons are made to larvae of *Attacus atlas* and *A. taprobanis* from nearby regions (Thailand, Sumatra, southern India). Field observations are given on oviposition, larval feeding and behavior, cocoon formation, and adult emergence. Larvae were reared from eggs on *Rhizophora apiculata, R. mucronata, Vitex glabrata,* and *Zanthoxylum. Attacus mcmulleni* is apparently multivoltine. *Anastatus* sp. (Hymenoptera: Eupelmidae), an egg parasitoid, was the only natural enemy found attacking the moth during this study.

KEY WORDS. Andamans, atlas moths, immatures, mangroves, *Rhizophora, Vitex, Zanthoxylum*

## INTRODUCTION

The genus *Attacus* Linnaeus (Saturniidae) is restricted to the Australasian region and comprises 14 known species, of which 11 are insular endemics (Peigler 1989). Moths in this genus include the largest species of Lepidoptera in the world. *Attacus mcmulleni* Watson, one of these insular species, is endemic to the Andaman group of islands. It was first described as a subspecies of *Attacus atlas* by J. H. Watson (in Packard 1914: 263-264, pl. 91) from specimens collected by W. R. McMullen on the island of South Andaman. In a revision of the genus, Peigler (1989) elevated it to the status of full species on the basis of characteristic and consistent differences in adult facies and genitalia. However, he stated that *A. mcmulleni* is the species that most closely resembles *A. atlas*. Peripherally isolated on the small islands of the Andaman Archipelago (Fig. 7), which are a minimum of 285 km from any continental land mass, and which never came into contact with the adjacent land masses during Pleistocene times when the sea level was lower (Ripley & Beehler 1989, Peigler 1989), *A. mcmulleni* is surmised to have speciated as a vicariant of *A. atlas*, the most widespread species of

the genus. A well-illustrated geographical glimpse of the Andaman Islands was given by Singh (1975).

Virtually nothing is published on the immature stages and life history of this moth. Pinned adults are rare in collections, with the exception of a series at The Natural History Museum, London. In addition, though the cocoons were briefly described by Watson (in Packard 1914), none were found in any of the major museums accessed by Peigler (1989). This study aims to fill these gaps in our knowledge of this little-known species.

## MATERIALS AND METHODS

Eggs and larvae were located visually on the host plants and collected along with a fresh sprig into transparent plastic containers, the size of which depended on the stage of the insect collected. The containers were cleaned of frass, wiped dry, and the larvae provided with fresh sprigs every day.

The eggs and initial instars were housed in small (8 cm diameter × 11 cm height) containers, while the later instars were reared in larger (9 cm × 19 cm) containers. The presence of head capsules in the rearing containers was used as the indicator for the determination of stadial lengths. This was possible as the larvae were not gregarious in any of the instars and so could be reared individually. All rearings were done indoors at ambient temperature and relative humidity which varied between 27.9 -33.4°C and 75 - 90.1%.

The mature larvae used either the sprig or the sides of the container to spin their cocoons and pupate. A stout twig was placed diagonally in the container to enable the emerging adult to climb up and expand its wings. All measurements were taken during the first cleaning of rearing containers following a molt. Voucher material from the rearing is deposited at the Entomology Section, Central Agricultural Research Institute, Port Blair, and in the Denver Museum of Natural History.

## RESULTS

### Host Plants and Habitats

*Rhizophora apiculata* Blume, *R. mucronata* Lamk. (Rhizophoraceae), *Zanthoxylum* sp. (Rutaceae) and *Vitex glabrata* R. Brown (Verbenaceae) are the four host plants on which eggs and larvae of *A. mcmulleni* were found. Larvae were subsequently reared on the same species as that on which they were collected.

While *V. glabrata* is a tree of moderate size in the inland deciduous forests of Middle Andaman, South Andaman and Long Island (all in the Andaman group of islands) (Parkinson 1923), *R. apiculata* and *R. mucronata*, which form the major component of the mangals (mangroves) of these islands, are found in mixed stands commonly fringing the tidal creeks as well as along the sea shores of many of the Andaman islands. It forms a wide belt of vegetation along the sea front, up to 2 km wide in some places and is regularly inundated by the tides.

Eggs, larvae, and cocoons of *A. mcmulleni* were collected from the mangals of Wright Myo, Wandoor, and Chiriyatapu in South Andaman and from Rutland. They were also collected from the inland semi-evergreen forest of Mount Harriet (South Andaman) up to an altitude of about 460 meters.

## Field Observations

The majority of the eggs and larvae that were collected came from the fringing mangrove habitat rather than from the inland forests. On each kind of host plant, all immatures were found on the tender terminal leaves. Eggs and larvae of the moth were found on both young and old trees of *Rhizophora*. In the mangrove habitat the immature stages were found in larger numbers on trees which were at the water's edge and not so much in the interior of the mangrove forest. Partially eaten terminal leaves signified the presence of larvae.

Eggs and first instar larvae were invariably found on the ventral surfaces of leaves on all the hosts. In a few instances however, eggs were found on the dorsal surfaces of leaves. Though one egg per leaf was the norm, up to four eggs were found on some leaves (Fig. 1). When more than one egg was laid per leaf, they were laid some distance apart ( = 0.24 cm between eggs, n = 5) and never in contact with each other.

On hatching the larva ecloses by making an irregular opening in the micropylar end. The larva does not eat the chorion fully and so half-empty chorions may be found attached to leaf surfaces long after larval eclosion.

The larvae in their early instars were found clinging along the midribs on the ventral surfaces of leaves, while the later instars shifted onto the terminal twigs, hidden between the leaves. In a few instances, first instar larvae were found side by side on the same leaf. However, later instars were never found together.

Up to the fourth instar the larvae, when at rest, bend their bodies such that the head end forms the short arm of the letter J. When the late instar larvae are disturbed they bend forward and tuck their heads beneath the thoracic segments and into the hollow formed by the thoracic legs which are bunched together and thrust forward.

Mature larvae feed inwards from the outer margin of the leaf and continue to feed whether the head is oriented upwards or downwards. Larvae stay on the tiny terminal branches and not on the leaves. One final instar larva that was collected from the field measured 11.8 cm in length.

The moths emerged from their cocoons at night in all the cases. In the two instances in which we observed emergence, it occurred between 1900-2030 hours. One virgin female was released on a coconut leaf a day after emergence at 0700 hours at Garacharma, South Andaman. This moth remained motionless without shifting its position for 48 hours and then disappeared.

**Oviposition:** Of the two reared females that were kept in cages, one

laid the first batch of eggs on the first night after emergence from the cocoon while the other laid its first batch of eggs three days latter. They laid a total of 200-223 eggs ($\bar{x} = 212$; $\sigma = \pm 16.3$) over a period of 10-11 days, when confined in cages and prevented from mating. One other virgin female laid 378 eggs in nine days from the date of emergence. All the eggs proved to be infertile. *A. mcmulleni* therefore conforms to the non-parthenogenetic nature of the Oriental Saturniidae, as both arrhenotokous and thelytokous saturniids have been reported from other regions of the world (Barlow 1982).

Barlow (1982) also stated that "the attraction and subsequent assembling of males to freshly emerged virgin females in fine wire-mesh boxes has been found to be very successful in temperate climes but this is yet to be tried out in South East Asia". Our attempts to attract males by taking newly emerged virgin females of *A. mcmulleni* in wire mesh cages to the Chiriyatapu mangroves proved futile.

**Phenology:** We collected and successfully reared the moths from eggs, larvae, and cocoons collected during the months of March, May, June, August, October, November, and October. Adults were also encountered during these months.

**Natural enemies:** The only natural enemy encountered was the egg parasitoid *Anastatus* sp. (Hymenoptera: Chalcidoidea: Eupelmidae). Only one wasp emerged from each parasitized egg; multiple parasitism was not observed in any of the cases. This chalcidoid genus was also reported as an egg parasitoid of *Attacus atlas* (Peigler 1989).

## Description of Immature Stages

The terminology for larval morphology is based on Peigler (1989). The measurements and durations of the various immature stages are given in Tables 1 and 2, respectively.

**Egg** (Fig. 1): Length 2.8 mm, width 2.4 mm, height 2 mm (n = 20). The oval egg, which is slightly flattened dorsoventrally, is dull white in color with polygonal punctations. It lies on its side embedded in a thick dry layer of orange-brown adhesive fluid. The micropyle is at one end from which radiates two narrow light brown, lateral bands and a dorsal teardrop shaped brown patch which is narrow at the micropylar end and broadens towards the center of the egg. All these brown markings have fuzzy edges and extend to a little beyond the midline.

**First instar:** Head glossy, deep brown; clypeus, labium, labial and maxillary palps, dull white; labrum brown. Body grayish-white in color with deep brown to black lateral markings which are most prominent on abdominal segments I to VII. This gives the larva the appearance of being striped when viewed laterally but not when seen dorsally. The proximal ends of dorsal scoli on thorax have five long brown spines arranged in an irregular circle with one similar spine a little off the apex of each scolus. All the other scoli too have spines with the maximum number on the subdorsal and lateral scoli. The distribution of scoli is identical to that of

Figures 1-6. *Attacus mcmulleni* 1. Eggs on *Zanthoxylum*. 2. Fourth instar 3. Sixth instar on *Rhizophora*. 4. Close-up of prolegs and triangular patch on anal proleg. 5. Cocoons 6. Adult male. Photographs by B. Pardhasaradhi.

*A. atlas* in this and all succeeding instars. Mealy matter (wax) is absent on this instar. The dorsum of the prothorax is plain white in front of scoli. There is a narrow brownish wavy line on the dorsum of anal plate along the contour of the anterior margin of the segment.

**Second Instar:** Immediately after molting it turns around and eats the molted skin as do all the other instars. Head creamish-yellow in color. Legs black, prolegs brown, clypeus and maxillary palpi white and labrum pale brown. Some setae on crotchets faint brown. Spines on scoli grey.

**Third/Fourth Instars** (Fig. 2): Labrum pale blue with a rough outer surface. Maxillary and labial palps also pale blue; dorsal and lateral surfaces covered with white powdery material that is thinner on the head

Table 1. Mean dimensions (cm.) of the various stages and of the head capsules of A. mcmulleni reared ex ovo in captivity in S. Andaman

| | Larval Instars (Lengths) | | | | | | Cocoon (L× W) |
| | I | II | III | IV | V | VI | |
|---|---|---|---|---|---|---|---|
| **Male** | | | | | | | |
| n | 3 | 4 | 4 | 6 | 7 | 8 | 3 |
| Length | 1.2 | 1.8 | 2.3 | 3.0 | 4.0 | 6.0 | 7.4 × 3.9 |
| ± S.D. | 0.12 | 0.06 | 0.05 | 0.18 | 0.18 | 0.73 | 0.6 × 0.5 |
| **Female** | | | | | | | |
| n | 1 | 1 | 1 | 2 | 3 | 3 | 3 |
| Length | 1.1 | 1.8 | 2.3 | 3.0 | 4.1 | 5.8 | 6.8 × 4.2 |
| ± S.D. | - | - | - | - | 0.2 | 0.4 | 0.4 × 0.3 |
| ***Male/Female** | | | | | | | |
| n | 2 | 4 | 4 | 6 | 6 | 5 | 5 |
| Length | 1.1 | 1.6 | 2.0 | 2.7 | 4.1 | · 5.9 | 6.× 23.0 |
| ± S.D. | - | 0.2 | 0.4 | 0.2 | 0.59 | 0.43 | 0.4× 0.3 |
| **Head Capsule** | | | | | | | |
| n | 11 | 6 | 9 | 10 | 11 | — | — |
| Length | 1.4 | 1.9 | 2.5 | 3.5 | 4.9 | — | — |
| ± S.D. | 0.04 | 0.08 | 0.09 | 0.09 | 0.23 | — | — |

*Represent pooled data as the sex of these moths was not determined.

than the rest of the body, the former having a black patch at its base. Spiracles narrow, long, very pale blue and located in a depression. Legs pale blue with black claws; prolegs light blue distally with black semicircular lines above the blue band on the third and fourth prolegs. Crotchets brown in color. Head smooth, pale yellow-green in color, with small white setae towards the mouth parts. Ventral surface pale blue-green including the inner aspect of the legs. The prominent saffron triangle on proleg encloses a pale grey-blue central region with a black band along the posterior margin.

**Fifth instar**: Head smooth, glossy, apple green in colour. Black irregular markings along inner margins of frontal sutures. Dorsal and sub dorsal scoli on thoracic segments reduced the stubs/warts. Spiracular scoli on thoracic segments black, and are the longest of all the scoli. Subspiracular scoli on abdominal segments I and II are small and black. Abdominal segments III to VIII also have small black scoli, but situated slightly lower than on segments I and II, in the subventral positions. The thoracic segments and the first two abdominal segments have a row of very short black scoli which are light blue basally. The surface of the body

Table 2. Mean durations (in days) of the various stages of *A. mcmulleni* reared *ex ovo* in captivity in S. Andaman

|  | Egg | I | II | III | IV | V | VI | Pupa |
|---|---|---|---|---|---|---|---|---|
|  |  |  | Larval Instars |  |  |  |  |  |
| **Male** |  |  |  |  |  |  |  |  |
| n | — | 3 | 4 | 4 | 6 | 7 | 8 | 8 |
| Duration | — | 3.3 | 5.0 | 6.0 | 6.5 | 8.6 | 15.8 | 25.8 |
| ± S.D. | — | 0.58 | 0.82 | 2.71 | 1.05 | 2.70 | 4.20 | 0.89 |
| **Female** |  |  |  |  |  |  |  |  |
| n | — | 1 | 1 | 1 | 2 | 3 | 3 | 5 |
| Duration | — | 4.0 | 5.0 | 6.0 | 6.5 | 9.0 | 19.0 | 28.0 |
| ± S.D. | — | — | — | — | 2.12 | 4.0 | 2.7 | 2.9 |
| ***Sex undetermined** |  |  |  |  |  |  |  |  |
| n | 3 | 5 | 6 | 4 | 5 | 6 | 4 | 3 |
| Duration | >5 | 7 | 6.2 | 8.3 | 9.2 | 10.5 | 19.5 | 34 |
| ± S.D. | — | 1.3 | 0.4 | 3.2 | 1.6 | 2.3 | 1.9 | 13 |

*Represents pooled data as the sex of these moths was not determined.

with green mottling, while the mottling on the anal segment is dark green to almost black.

**Sixth Instar** (Figs. 3-4): Head, especially vertex smooth, glossy green. A thin layer of white mealy matter on the frons and a little on the sides of the epicranial suture, otherwise the head is devoid of mealy matter. An irregular black patch at base of labium. Mandibles black; clypeus, labrum, labium, maxillary and labial palps pale blue. Labial palps with an annular black ring. Frontal sutures black. Ventral surface green, legs and prolegs deep black in colour on the outer surface with sparse grey setae. Crochets dark brown. An anterior bluish-white stripe in the black area of the prolegs. Spiracles pale blue. The pink triangle on anal claspers (Fig. 4) more oval in shape than in the earlier instars and less intense (paler) in color. The enclosed space is not dirty green as in earlier instars but a pale, dirty green with brownish-black pits. All along the outside of the rear margin is a deep black band. The whole larva is mottled, with the mottling becoming quite dense on the anal triangle.

**Pupa:** Length 5.4 cm, width 2.0 cm (n = 2). Deep brown in color; cremaster also deep brown, prominent and blunt, ca. 3.8 mm long and 2 mm wide (at the widest point).

**Cocoon** (Fig. 5): The cocoon is coarse; brownish in color with a long peduncle. Cocoons were usually found individually webbed onto leaf surfaces, though in a few instances two cocoons were found together (Fig. 5). The mean length of the peduncle was 7.0 cm (range 4.5-10.5 cm; n =
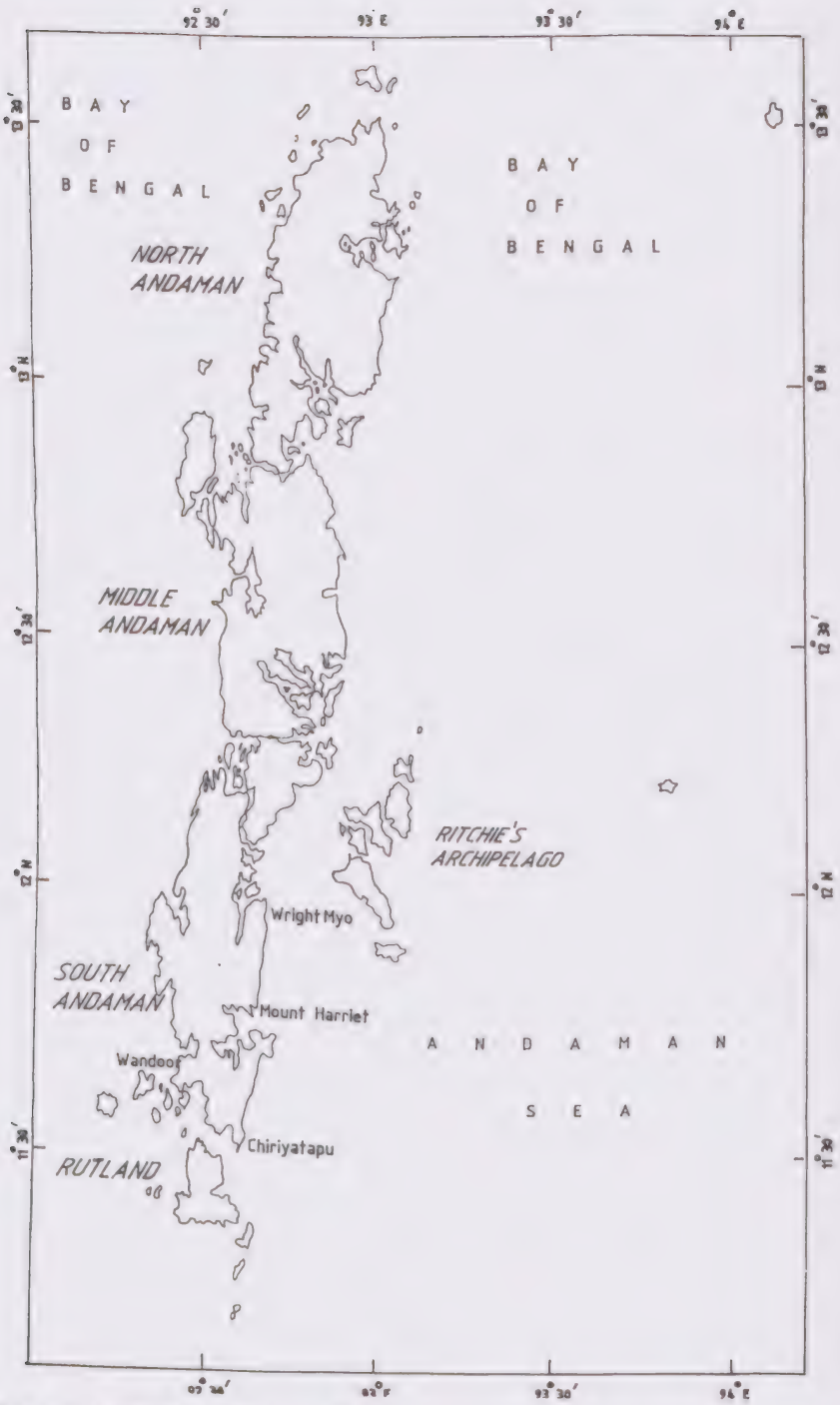
Figure 7. Map of Andaman Islands.

11) while the mean length of the cocoon proper was 7.3 cm (range 6.5-9.5 cm; n = 18) and its mean width 3.8 cm. (range 2.9-4.5 cm; n = 17). The mean weight of the empty cocoon exclusive of pupal case is 0.959 ± 0.11 g ranging from 0.76 to 1.039 (n = 5).

The adult moth (Fig. 6) was described in detail by Peigler (1989), and a male was illustrated in color.

## DISCUSSION

Over 100 plant species belonging to 90 genera in 48 families have been reported as host plants of *Attacus* spp. (Peigler 1989). However, Peigler was unable to assign a botanical name to the plant on which larvae and cocoons of *A. mcmulleni* were collected by McMullen, as Watson (in Packard 1914) used only the vernacular name of the plant viz., "samalu". This we now know to be *Vitex trifolia* (Verbenaceae), a widely grown hedge plant in the Andamans which was introduced from mainland India prior to 1866 (Prain 1890, Parkinson 1923).

Villiard (1969) was of the opinion that greater success on the rearing of *Attacus* larvae—particularly the later instars—could be achieved by feeding them on a mixed diet. In the current study we were unsuccessful at inducing larvae of *A. mcmulleni* to switch diets. Larvae reared initially on *Rhizophora* spp. were switched to *V. trifolia* and to *V. glabrata*. All attempts proved futile though individuals collected on *V. glabrata* completed their life cycles on leaves of the same species.

Peigler (1989) recorded no species of mangroves as host plants of *Attacus*. Murphy (1990) was the first to mention the presence of *Attacus* in mangrove habitats, stating that *Attacus atlas* "occurred once [on *Avicennia alba* B1., Avicenniaceae] simultaneously with many other trees" and that it occurred at low levels on *Bruguiera gymnorhiza* (L.)Lamk., (Rhizophoraceae). Nevertheless, this is the first time that a species of *Attacus* has been found to be able to complete its life cycle on a species of Rhizophoraceae. Species of *Attacus* were previously known to utilize Verbenaceae and Rutaceae (Peigler 1989). Our studies also indicate that *Rhizophora* spp. are preferred to *Vitex glabrata* and *Zanthoxylum* by *A. mcmulleni*.

Like *A. atlas*, *A. mcmulleni* also consistently passes through six larval instars in its life cycle. Although *A. mcmulleni* probably has a wider host range than that discovered by us, we feel that in the species-poor mangrove habitat (with plant species diversity markedly lower than in other moist tropical habitats) with a preponderance of *Rhizophora* spp. in closely packed stands, neither the ovipositing female nor the larvae should have any difficulty in finding host plants. Nevertheless they lay only a few eggs at each oviposition site which Janzen (1984) believed is normal behavior for polyphagous species.

Watson (in Packard 1914) quoting McMullen, stated that "there are least two broods per year" with May and July being the two months which the moths were collected. Judging from the various stages of *A*.

*mcmulleni* that we have collected during various months from the field, it is definitely not bivoltine but is multivoltine and in all probability flies throughout the year.

The eggs and cocoons of *Attacus memulleni* are probably indistinguishable from those of the allied species. The larvae are also almost identical to those of some populations of *A. atlas* (see Lampe 1984; Paukstadt & Paukstadt 1984a, b, 1986; Peigler 1989), but a few minor differences were noted as follows.

Larvae of *A. atlas* from western Java and some of the species from the Philippines have solidly orange shields on the anal prolegs. These shields on larvae of *A. atlas* from Thailand and Taiwan and *A. taprobanis* from Sri Lanka and southern India are rimmed with orange and have green centers. Larvae of *A. mcmulleni* are intermediate; the shield appears solidly orange at first glance, but a faint green center is visible upon closer examination. In *A. mcmulleni* the subspiracular scoli are blue proximally and blackish distally, like those of *A. taprobanis* and *A. atlas* from Taiwan and Thailand. The white waxy covering in *A. mcmulleni* is as dense or denser than in any of the other species of *Attacus*.

## LITERATURE CITED

BARLOW, H. S. 1982 [1983]. An introduction to the moths of South East Asia. Malayan Nature Soc., Kuala Lumpur. ix + 305 pp., 50 col. pls.

JANZEN, D. H. 1984. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. Oxford Surv. Evol. Biol. 1:85-140, 4 col. pls.

LAMPE, R. E. J. 1984. Die Präimaginalstadien von *Attacus atlas sumatranus* Fruhstorfer im Vergleich mit *Attacus atlas* Linnaeus von Taiwan (Lep.: Saturniidae). Entomol. Z. 94: 161-167.

MURPHY, D. H. 1990. The natural history of insect herbivory on mangrove trees in and near Singapore. Raffles Bull. Zool. 38: 119-203.

PACKARD, A. S. 1914. Monograph of the bombycine moths of North America, part 3 (edited by T. D. A. Cockerell). Mem. Natl. Acad. Sci. 12: ix + 1-516.

PARKINSON, C. E. 1923. A forest flora of the Andaman Islands. Bishen Singh
     Mahendra Pal Singh, Dehra Dun. (Reprint). 325 pp.

PAUKSTADT, U. & L. H. PAUKSTADT. 1984a. Beitrag zur Kenntnis der Ökologie und
     Biologie von *Attacus atlas* Linnaeus 1758 aus westjavanischen und
     balinesischen Populationen (Lep.: Saturniidae). Entomol. Z. 94: 225-240.

—— 1984b. Beschreibung und Abbildung der Präimaginalstadien von *Attacus
     atlas* Linnaeus 1758 aus thailändischen Populationen (Lep.: Saturniidae).
     Entomol. Z. 94: 273-283.

—— 1986. Beschreibung der Praeimaginalstadien von *Attacus taprobanis*
     Moore 1882 aus singhalesischen Populationen sowie Angaben zur Ökologie
     und Biologie (Lepidoptera: Saturniidae). Nachr. Entomol. Ver. Apollo,
     Frankfurt (N. Ser.) 7: 71-90.

PRAIN, D. 1890. The non-indigenous species of the Andaman flora. J. Asiat. Soc.
     Bengal 59: 235-261.

PEIGLER, R. S. 1989. A revision of the Indo-Australian genus *Attacus*. Lepid. Res.
     Found., Inc., Beverly Hills, Calif. xi + 167 pp.

RIPLEY, S. D. & BEEHLER, B. M. 1989. Ornithogeographic affinities of the
     Andaman and Nicobar islands. J. Biogeogr. 16: 323-332.

SINGH, R. 1975. The last Andaman Islanders. National Geographic 148(July):
     66-91.

VILLIARD, P. 1969. Moths and how to rear them. Funk & Wagnalls, New York.
     242 pp.

# Rediscovery of the endangered Palos Verdes blue butterfly, *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel (Lycaenidae)

Rudi Mattoni

Department of Geography, UCLA, Los Angeles, CA 90024

**Abstract.** The Palos Verdes blue butterfly (PVB) was believed extinct for eleven years when a small colony was rediscovered by accident on March 10, 1994 at a site from which it had not been recorded earlier. The systematics and natural history of the species (=subspecies for conservation purposes), its historic and present habitat, and plans necessary for its recovery are discussed.

## INTRODUCTION

The Palos Verdes blue butterfly (PVB) was believed extinct for eleven years when a small colony was rediscovered by accident at a site from which it had not been recorded earlier. The rediscovery on March 10, 1994 was made by the team of Rick Rogers, Timothy Dahlum and Rudi Mattoni while visiting the Defense Fuel Support Point (DFSP) at San Pedro for other purposes. The subspecies was believed extinct by at least two authors, Arnold (1987) and Mattoni (1993). The following paper summarizes information to date for the PVB, its habitat and natural history, outlines recommendations for recovery of the species, and discusses what has been done to date.

## HISTORICAL PERSPECTIVE
### Systematics

The subspecies was described by Perkins and Emmel (1977) from Los Angeles county just prior to its listing among the second group of butterflies to be legally recognized as endangered by the federal Endangered Species Act. The taxon was diagnosed as a subspecies of the silvery blue, *Glaucopsyche lygdamus,* a polytypic species comprised of at least 10 valid subspecies that are usually found in small closed local colonies across most of North American north of Mexico and extending into easternmost Siberia. There it meets with its sister species, *G. alexis*, of which *G. lygdamus* and its suite of subspecies might all be considered subspecies within a large holarctic complex. Nothing is known about the border area of these taxa, but at the very least relationships are complex. The PVB was originally differentiated from its likely sister subspecies, *G. lygdamus australis*, the southern blue, by exclusive use of the milk

Figure 1. Specimens of the PVB and the southern blue showing patterns of UNS variation. PVB right column, southern blue left column, single females of PVB, right, and southern blue, left, showing mean differences in blue overlay on the black ground color. PVB females usually lack all but a trace of basal blue.

vetch or rattleweed, *Astragalus trichopodus lonchus*, a relatively fast flight in comparison to *australis*, an earlier flight period than *australis*, and several wing characteristics including a slightly darker underside ground with larger macules well set off by white halos (Figure 1).

## Conservation Interest

The butterfly was geographically circumscribed as a coastal terrace ecotype found only on the southern half of the Palos Verdes peninsula in southern Los Angeles county (Figure 2). The species had high conservation value and was not officially delisted in spite of the strong evidence that the species was extinct after 1983. During this period all building

Figure 2. Map of the Palos Verdes peninsula showing the known distribution of the PVB on the south slope before its disappearance, 1979-83. The numbers reference specific sites where the butterfly was observed, see text. Data collected by Jess Morton. The inset map of California positions the Palos Verdes peninsula.

projects in the species distribution area were required to recognize habitat value. The recent find will permit artificial reintroduction of the species into former habitats that can be enhanced following a proper revegetation plan. This will assure both a much higher probable survivability of the PVB and an expanded coastal sage habitat over what now exists across the peninsula.

## Distribution

By the time of its discovery in the early 1970's by Perkins, the PVB was already reduced to the few habitat fragments that retained some natural characteristics. In 1981 and 1982 the 12 then known PVB sites were mapped by Jess Morton (Figure 2). The DFSP San Pedro site was unknown. Three of the sites, Hesse Park, Alta Vista, and San Pedro Hill, were razed as habitat between 1978 and 1985, well after they were isolated. The remaining colonies were partially discrete and occurred within three contiguous open spaces that were largely covered with native coastal sage scrub: Agua Amarga (2), landslide moratorium (10, 11, 12), and Palos Verdes Drive East (4-8). Each of the numbered colonies were isolated by anthropogenic land fragmentation and were

Figure 3. Map of the Palos Verdes peninsula indicating the known distribution in 1994 of Astragalus *tricopodus* (A), *Lotus scoparius* (L), and "open" space that could potentially be restored as habitat. Open space is indicated by stippling. Trapping stations for the general arthropod census are indicated by the circles.

not discrete in the sense of natural metapopulations, possibly excepting the last set. Palos Verdes Drive East was, and to large extent remains, essentially continuous habitat. The last known PVB occurrence was 1983, when Morton and his volunteers noted a few specimens, mostly at Palos Verdes Drive East. There are no earlier data available so the only possible description of distribution is extrapolation from historic plant community information which itself is largely conjectural. Gales (1988) and Brinkmann-Busi (1992) have produced floras of the area.

The largest known populations during the brief time span the PVB was monitored were at Alta Vista Terrace (type locality), Hesse Park, and among the scrub extending from Palos Verdes Drive East to Friendship Park. Alta Vista was built over in 1978. Population sizes were never estimated, but by the early 1980's numbers were extremely low with probably less than 300 adults among all remaining fragments. At Hesse Park in spring, 1982, I counted six adults on the best day, with some 20 foodplants. Each plant had at least 100 eggs, and one plant over 500. Foodplant availability was limiting due to spring discing for fire suppression.

## Habitat and ecology

Adult butterflies of all silvery blue subspecies are closely associated with their legume larval foodplants. Recorded foodplants include many species in the genera *Lupinus*, *Vicia*, *Lathyrus*, *Lotus*. *Melilotus*, *Medicago*, *Oxytropis*, *Thermopsis*, and *Astragalus* (Scott, 1986). In general, a silvery blue butterfly population at any one locality is restricted to a single plant species. The reason often invoked for this specificity is local adaptation of larvae to particular suites of alkaloids that each plant species presumes to produce for defense. Breedlove and Ehrlich (1972) provided evidence consistent with this hypothesis of coevolution for the case of the Rocky Mountain subspecies of the silvery blue and its *Lupinus* foodplant hosts. However, the general concept of insect/foodplant specificity and the coevolution paradigm is far from convincing (Jermy, 1993 and references).

The PVB is a coastal sage associated ecotype, originally believed restricted to the milk vetch as foodplant. The vetch was largely confined to the summer fog belt characteristic to the southern exposures of the Palos Verdes peninsula at elevations between 100 and 300 meters. The historical area probably occupied by both *Astragalus* and the PVB was about 5000 ha. The flora of the northeast slopes of the peninsula included the low shrub legume, *Lotus scoparius*, foodplant of the sister subspecies *G. lygdamus australis*. The distributions of both vetch and deerweed found in 1994 are mapped on Figure 3. Other open sites of greater size than 20 ha are also indicated, these being potential sites for reintroduction of the PVB after appropriate habitat revegetation. Many smaller fragments remain, but these are too vulnerable to be of conservation value.

Whether *australis* was either historically or recently parapatric with *palosverdesensis* is unknown, although genetic isolation of the subspecies most likely occurred no later than the end of the last ice age, about 10,000 years ago, when the coastal sage scrub of the Palos Verdes peninsula became isolated from the nearest scrubland to the north by the Los Angeles plain and extensive marshland. It is noteworthy that although both the vetch and deerweed occur on Santa Catalina island, the silvery blue is not found there (the butterfly occurs on both Santa Rosa and Santa Cruz). Other biogeographical evidence suggests that Santa Catalina had close affinity to the Palos Verdes peninsula, although there was no physical connection during the past few glaciations.

## Causes of presumptive extinction in 1983

In 1983 the last sightings, of between 4 and 7 individual PVB, were made. The discrepancy in number was the likely result of multiple sightings. The number sighted was low by any criteria, supported by many unsuccessful survey days in the field. Thereafter intensive searches by several local lepidopterists were made for several years without success (Arnold, 1987; J. Morton, pers. comm.). The ultimate cause of

extinction was probably destruction of natural coastal sage scrub communities by a combination of development and fire suppression tactics producing ever increasing fragmentation of the remaining natural ecosystem. For organisms with extremely sedentary demographics, population dynamics obviously became disrupted. Some contribution was also made by illegal overcollecting of early stages by a zealous local collector community.

The historic PVB population was likely continuous across the 5000 ha coastal scrub habitat that covered the south half of the peninsula. With intensive development since 1950, habitat was greatly reduced and fragmented, although the 500 ha landslide moratorium area section of open space remains (1994). This section (Figure 3, south-center portion) is not continuous quality habitat, however, but is a mosaic of coastal sage scrub assemblages interspersed with disturbed patches of farmland and otherwise disced and exotic plant contaminated zones. Clearing practices so degraded habitat values for the butterfly that the 1982 construction at Hesse Park, performed by the city of Rancho Palos Verdes in violation of the federal Endangered Species Act, directly destroyed what was probably the second largest remaining PVB colony. The city was subsequently sued by the federal government under the Endangered Species Act, but this legal action was dismissed under the theory that a city could not be held liable.

The proximate cause of PVB extirpation was probably climatic. The winter of 1982-83 was cold and extremely wet, followed by the winter of 1984 that was cold and dry and the beginning of a major drought. With fragmented populations, Hesse Park habitat destruction, and probable overcollecting, the diminished bank of diapausing pupae either did not survive or produced so few adults that maintaining population size was impossible. Simultaneously foodplant numbers declined as well (J. Morton, pers. comm.). Arnold (1987) reported the apparent disappearance of the species and speculated it became extinct. Mattoni (1990, 1993) later concurred with this view.

## CURRENT STATUS
### Present distribution
Immediately following discovery of the PVB at San Pedro, a thorough search was conducted across all sites indicated on Figure 3; sites where both vetch and deerweed were known. Neither adults or any early stage signs were found on vetch. Presence of either eggs and larvae on the vetch foodplant can be easily observed. The most likely additional localities were hypothesized to be on the stand of vetch at the west end of the landslide area (center of map, Figure 3) and on deerweed in upper Malaga canyon (Figure 3). Observations at both localities were negative. In all likelihood the sole remaining population of the PVB occurs at the San Pedro DFSP.

### Regional foodplant distribution

*Lotus scoparius* is presently found at several localities on the penin-
sula (Figure 3). Excepting a few plants on the Malaga beach sand dune,
all populations are on the north facing slope of the peninsula from
Malaga canyon south to the San Pedro DSFP. These populations are
associated with the more mesic, dense scrub community of the north
slopes. Additional plants may yet be discovered, but these will surely be
few and isolated. At San Pedro the majority of plants are found on
disturbed sites, either slopes graded within the past few years, mowed
roadside, or landscaped slopes.

In contrast, the vetch, *Astragalus tricopodus lonchus*, has only been
observed across the south slope of the peninsula in more open xeric
coastal sage scrubland. The species is associated with open scrub,
implying it may not compete well in establishing within dense mature
stands. However, in the most "natural" of the mature scrubland at San
Pedro, the species occurs within dense California sage formations. Here
mature vetch plants, reaching to nearly a meter in height, are supported
by sage branches. The condition permitting occurrence in an otherwise
dense cover may be small animal activity (e.g. rabbit trails) that provide
periodic openings for vetch seedling establishment. Seeds of *Astragalus*
are known to have longevities to a century (R. Snow, pers. comm.).

Presence of the two foodplants together at Palos Verdes is only known
at San Pedro. Two exceptions, one vetch in a north slope canyon and one
deerweed in the landslide area were observed by Brinkmann-Busi (pers.
comm.), but the findings followed several years of observation. The
reasons for the usual mutual exclusion are unclear as the two plants are
together in the Santa Monica mountains and were both found earlier on
the El Segundo sand dunes and coastal prairie. The vetch is always the
less abundant species, but seems relatively more abundant where
topoclimates are severe.

### Bionomics of the PVB

Larvae of the silvery blue are ant tended and usually strongly associ-
ated with ant species, three of which were recorded by Ballmer and Pratt
(1992). Developing PVB larvae usually feed almost entirely inside
rattleweed seedpods, using the seeds for nutrition, this plant part being
very high in protein and fat. The presence of a larva within a pod is
indicated by an entry hole made by the larva. Larvae have not been
observed on deerweed, but they certainly are external feeders on flowers
and seedpods because deerweed seedpods are smaller than larvae. Ants
specific to the PVB are unknown, but there is unquestionably an ant-
larva association. In vetch ants gain access by utilizing the larval entry
hole and the larvae are ant tended for the last two instars. At least ten
ant species have been found at the new locality to date including two,
*Iridomyrex humilis* and *Formica pilicornis*, that are known associates of
*Glaucopsyche lygdamus* subspecies (Rogers and Snelling, pers. comm.).

The importance of ants in protecting *G. lygdamus oro* was experimentally demonstrated by Pierce and Easteal (1986) who found 45-84% lower parasitism levels among ant tended larvae. The general phenomenon of ant associations with lycaenid butterflies was reviewed by Fiedler (1991). Determination of the ant hosts should be a high priority given the low surviving PVB population.

The PVB is single brooded. Populations known from the south slope had adult flights recorded from late January into March. Eggs were usually laid on flowerheads of the foodplant, but when foodplant numbers were reduced just prior to the 1982 extinction, eggs were laid over the entire plant. The final generation observed at Hesse Park had larvae feeding on leaves because flowerheads and seeds were exhausted.

Three other Lycaenid butterflies were associated with the vetch flowerhead/seedpod guild: *Strymon melinus, Leptotes marina* and *Everes amyntula*. The first two are polyphagous, have many alternate foodplants, and remain widespread species across the Palos Verdes peninsula as well as globally. The latter is an oligophage that was restricted to *Astragalus* at Palos Verdes. It uses other species of legumes elsewhere. The species was believed extirpated from the Palos Verdes peninsula. After a ten year hiatus, the species was sighted near site 4, Figure 2 in 1995 (G. Pratt, pers. comm.).

The western tailed blue, *Everes amyntula*, occurs on at least four channel islands, including Santa Catalina. In contrast *Glaucopsyche lygdamus* is only found on two islands. Given the pattern of foodplant distribution with both deerweed and vetch found on the four islands of occurrence, it is unclear why the silvery blue is not found on all the islands. Its potential capability of using two foodplants would provide greater buffering against adverse conditions and is certainly the factor responsible for survival of the PVB at San Pedro while the western tailed blue was lost.

We first observed PVB females at San Pedro ovipositing on deerweed, exclusively using flowerheads. Later Rogers saw females ovipositing on vetch and discovered eggs on vetch inflorescences. Eggs are easily observed on flowers and seedpods in contrast to those on deerweed. We have no information on selectivity of individual females to either plant. It has recently been demonstrated for other butterflies that individuals exhibit behavioral specificity in the presence of multiple foodplants (review in Papaj and Lewis, 1993).

Two other dominant spring flying butterflies at the site, the California green hairstreak (*Callophrys affinis perplexa*) and the funereal dusky wing (*Erynnis zarucco funeralis*), both use deerweed as foodplant. However, their larvae are leaf feeders and thus avoid interference competition with early stages of the PVB. Females of these species deposit eggs upon stems and leaves. Hairstreak larvae are not ant-tended lycaenids.
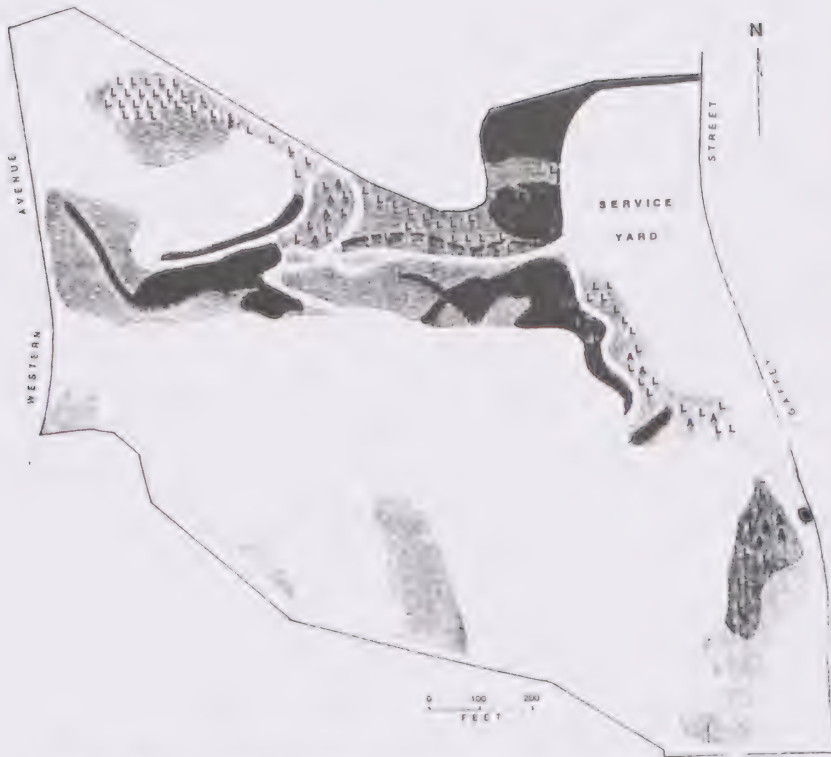
Figure 4. Map of the San Pedro DFSP presenting an overview of "native" habitat (heavy stippling) and degraded open space habitat that has potential for restoration (light stippling). Locations of individuals or stands of Astr*agalus tricopodus* and *Lotus scoparius* are indicated by the letters A and L respectively. The clear areas position underground storage tanks and are unsuitable for revegetation. The broad line extending from Western Avenue easterly, dashed in the central portion, indicates the riparian seasonal stream with mature willows (solid line) and sporadic *Baccharis* (dashed line).

## The San Pedro colony

While setting out and servicing pitfall and yellow pan traps in late 1993 for a regional arthropod survey we noted that the DFSP San Pedro site did not appear likely to support a PVB population. Discovery of the PVB at all was unexpected. PVB use of deerweed was unknown and the vetch population we noted was a cluster of fewer than 25 individuals. We subsequently found a second cluster with another 30 individuals. A proximate vegetation map of the site (Figure 4) shows the distribution of deerweed, vetch, and coastal sage scrub across both relative "natural" and disturbed open space. The latter areas should be revegetated to create a coastal sage plant community and augmented habitat.

Figure 5. Map of butterfly transect, pitfall traps, and yellow trap stations at San Pedro
DFSP, superimposed over figure 6. Eight segments of the transect are
indicated by lines drawn across the transect with the segment number
given. Segments 4, 5, and 8 required retracing of the walk over all or part
of the transect segment. Counts were only recorded on the outbound walk
on those portions of the segment.

After sighting the butterfly and notifying the U.S. Fish and Wildlife
Service, we immediately instituted a transect walk survey to provide
semi-quantitative data on the PVB. Figure 5 is the vegetation map with
an overlay showing the transect route selected for observing the PVB
(and other readily identifiable insects) as well as the locations of
trapping stations. Only the westerly two trap stations were in operation
when the butterfly was discovered. We have since expanded our survey
plan for the site.

## PVB population size and distribution

The transect was delineated to traverse the majority of foodplant
concentrations (Figure 5). No PVB were observed beyond the envelope
of foodplants. We assumed the species to be highly sedentary and seldom

moved beyond foodplant sites by more than a hundred meters. All tests with related species of blue butterflies demonstrated restricted flight ranges (Arnold, 1983; Pollard and Yates, 1993; Keller et al. 1966).

The transect was sampled by one individual, R. Rogers, about three times a week from March 12 to April 11. Data were recorded on a small scale map where every visually identifiable insect was noted. The transect was about 950 m (3050 ft) in length. Individuals recorded included all in view, usually within 10 meters either in front of or alongside the observer. The usual 5 m square forward "projected box" of the Pollard method (Pollard and Yates, 1993) would have yielded too few observations. Care was exercised to not record any insect twice on any transect leg. The observer was highly trained and experienced in the methodology.

The data are given in Table 1, including two other butterflies in flight during the time period, the California green hairstreak and the funereal dusky wing. Sampling was made in the morning and afternoon on most days. The last PVB was sighted April 8, with an exception seen by J. Morton on April 23. A total of 13 days were sampled for a total of 24 samplings. For analysis the transect was arbitrarily divided into 8 segments, shown on Figure 5. Each segment was fairly uniform with respect to vegetation and slope, characteristics briefly stated on Table 1. The number of individual male and female PVB, hairstreaks, and dusky wings are presented with their relative frequencies along each transect segment.

The results show a highly significant nonrandom distribution of the three most common spring butterflies among the different transect segments. A most striking feature was segment 1, which represents an early succession vegetative cover with deerweed dominant and forming an almost pure stand in the shrub profile: the PVB was not seen at all, while the California green hairstreak occurred on no other segment. Segment 2 was low quality habitat and probably served only as a corridor, if not a barrier. Even the dusky wings were not observed while they otherwise were randomly distributed across all other segments.

The PVB had its highest occurrence where deerweed was robust (segments 4, 6 and 7) and vetch relatively abundant (6). The low female sex ratio (0.26) is not unusual among lycaenids in nature and is in all likelihood a sampling artifact. Females are less vagile, devoting most time to siting oviposition locations. The absence of PVB from the segments 1 and 2 implies sensitivity to the low cut sward of 2 that may form an absolute barrier to movement .

Because of methodological defects in using marking as a demographic tool with lycaenid butterflies (Murphy, 1988) and acute concerns when they are endangered, population size estimates can only be crudely approximated by using transect counts. If we assume the maximum number counted on the best of the two walks are each different individuals, each set between days sampled represent new eclosions, that the

Table 1. Total number of butterflies observed on the transect walks at the San Pedro DFSP, March 12 through April 11, 1994. An additional female was seen on the site by another observer on April 23 and another transect walk was made April 29, at which time all spring species were absent. Three spring species are included, with males and females indicated for the Palos Verdes blue, *Glaucopsyche lygdamus palosverdesensis* (PVB). The other two species are the funereal dusky wing skipper, *Erynnis zarucco funeralis* (FUN) and the California green hairstreak, *Callophyrs affinis perplexa* (CAG). The length of each transect segment is given in meters as is both total number (numerator) and relative frequency (denominator, boldface) of each category along each segment (number/meters).

| Segment | Description of habitat | length (m) | PVB ♂ | PVB ♀ | FUN | CAG |
|---|---|---|---|---|---|---|
| 1 | in early succession, predominant *Lotus scoparius* excavated soil deposit, sandy, | 150 | 0 | 0 | 22 **.15** | 21 **.14** |
| 2 | open mown corridor, Mediterranean grass with few seedling *L. scoparius* | 65 | 1 **.01** | 0 | 0 | 0 |
| 3 | disturbed pipeline right-of-way, dense *L. scoparius* growth, *Encelia* present, the entire section does not appear natural | 130 | 4 **.03** | 3 **.02** | 9 **.07** | 0 |
| 4 | slope appears unnatural with high clay, rocks, and rubble, buckwheat appears planted, few *L. scoparius* robust | 70 | 15 **.21** | 4 **.06** | 1 **.01** | 0 |
| 5 | natural appearing coastal sage slope, few *L. scoparius*, robust, shrub community diverse | 100 | 9 **.09** | 9 **.09** | 2 **.02** | 0 |
| 6 | east side of road myoporum landscaped slope with mix of *L. scoparius* and *Astragalus*, west side native dense coastal sage | 145 | 39 **.27** | 10 **.07** | 21 **.15** | 0 |
| 7 | contoured slope landscaped with sparse myoporum, interspersed with *L. scoparius* and *Astragalus*. | 115 | 12 **.10** | 7 **.06** | 22 **.19** | 0 |
| 8 | dense native coastal sage scrub with sparse *L. scoparius* and *Astragalus*. | 175 | 0 | 0 | 3 **.02** | 0 |
| Totals | | 950 | 80 **.08** | 29 **.03** | 117 **.13** | 21 **.02** |

numbers of females is the same as males, and that we only observed 20% of the real population, then Nt would be about 300 and Ne somewhat less. This is likely an overoptimistic value.

## Conservation planning

By any measure this last remaining population of the PVB is small and in jeopardy of extinction from stochastic processes at any time within the next decade. Because of the degraded state of remnant natural habitat at the DFSP, it will be necessary to implement a habitat conservation plan as rapidly as possible. As an emergency step we recommend an immediate captive breeding program be instituted to both guarantee that the population is not lost and to provide a significant increase in numbers for later release at former known sites of occurrence. Methodology for mass rearing the PVB was developed a decade ago using the southern blue as a surrogate in hopes of then preventing extinction of the PVB (Mattoni, 1988). Recovery of the species will only be possible by establishing several discontinuous colonies distributed across all large remnants of the butterfly's former range.

## Habitat revegetation

The first step towards recovery will be to maximize survival potential for the butterfly at the San Pedro DFSP. The fundamental philosophy will be a coastal sage community revegetation plan that emphasizes ecosystem integrity and not single species requirements. Preliminary discussion with DFSP indicates that land will be available for restoration. About 100 acres of the site are suitable (Figure 4) including the approximate 30 acre native plant community fragments. The latter provide both model data for a restoration plan and a source of propagules for restocking.

The proximate general plant community cover was mapped by Brinkmann-Busi and Mattoni to provide one basis of habitat restoration. Brinkmann-Busi prepared a detailed inventory of the flora, surveyed several 100 m transects that indicate plant densities across the major topological aspects of shrub cover, and completed detailed vegetation maps of the area involved with pipeline maintenance. Replacement of a major pipeline that bisects the butterfly population on site 3 was underway when we first found the PVB. Completion of construction is necessary as the least damaging alternative for the site because the original pipe was near failure, an environmentally unacceptable event that would release large quantities of petroleum product into the habitat. Construction can continue with virtually no impact on the PVB or other natural values and will provide greater overall habitat value if care is taken to minimize impact on the butterfly and the area is correctly revegetated.

**Regional reintroduction**

The ultimate goal will be to reintroduce the PVB into all of its former sites. Before this can be successfully undertaken, however, the plant communities must first be substantially enhanced with special attention given to their nuances of assembly relative to topoclimates and substrates. Accurate vegetation maps are necessary for this purpose, but many political hurdles need to be addressed including regional planning. An attempt is underway to establish a Natural Community Conservation Plan (NCCP) for the Palos Verdes peninsula to shape habitat conservation in the region. Until there is political resolution of a rather convoluted land use situation that involves participation of five municipalities, further biological discussion is not useful except to point out that the PVB is one of the few known Palos Verdes endemics and must be reckoned with under present laws.

## LITERATURE CITED

ARNOLD, R. A. 1983. Ecological studies on six endangered butterflies: Island biogeography, patch dynamics, and design of habitat preserves. Univ. Calif. Public. Entomology 99:1-161.

—— 1987. Decline of the endangered Palos Verdes blue butterfly in California. Biol. Cons. 40:203-217.

BALLMER, G. R. & G. F. PRATT. 1992. Quantification of ant attendance (Myrmecophily) of lycaenid larvae. Jr. Res. Lepid. 30:95-112.

BREEDLOVE, D. & P. R. EHRLICH. 1972. Coevolution: patterns of legume predation by a lycaenid butterfly. Oecologia (Berl.) 10:99-104.

BRINKMANN-BUSI, A. 1992. Flora of the Palos Verdes Peninsula, a preliminary checklist. Privately published.

FIEDLER, K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (insecta: Lepidoptera, Papilionidae) Bonner Zool. Monographen No. 31. 210 pp.

GALES, D. 1988. Handbook of wildflowers, weeds, wildlife, and weather of the south bay and Palos Verdes peninsula. Privately published.

JERMY, T. 1993. Evolution of insect-plant relationships - a devil's advocate approach. Entomol. exp. appl. 66: 3-12.

KELLER, E., R. MATTONI, M. SEIGER. 1966. Preferential return of artificially displaced butterflies. Animal Behavior 14:197-100.

MATTONI, R. H. T. 1988. Report to California Department of Fish and Game, Contract C-1456.

—— 1990. Butterflies of greater Los Angeles. Lepidoptera Research Foundation, Beverly Hills, CA.

—— 1993. The Palos Verdes Blue, *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel. in T. R. New, editor. Conservation Biology of Lycaenidae (butterflies). IUCN Species Survival Commission No. 8, Gland, Switzerland.

MURPHY, D.D. 1988. Are we studying our endangered butterflies to death? Jr. Res. Lepid. 26:236-239.

PAPAJ, D. & A. C. LEWIS. eds. 1993. Insect learning: Ecological and evolutionary perspectives. Chapman and Hall.

PERKINS, E. M. & J. F. EMMEL. 1977. A new subspecies of *Glaucopsyche lygdamus* from California (Lepidoptera: Lycaenidae). Proc. Ent. Soc. Wash. 79:468-471.

PIERCE, N. & S. EASTSEAL. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. J. Animal Ecol. 55: 451-462.

POLLARD, E. & T. J. YATES. 1993. Monitoring butterflies for ecology and conservation. The British butterfly monitoring scheme. Chapman and Hall, London.

SCOTT, J. A. 1986. The butterflies of North America. Stanford. Palo Alto.

# Mortality of *Anaea ryphea* (Lepidoptera: Nymphalidae) Immatures in Panama

Astrid Caldas

Departamento de Biologia Animal e Vegetal - IB, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, RJ 20559-900, Brazil

**Abstract.** In order to assess the main mortality factors acting on immature stages of *Anaea ryphea* in Panama, I censused a population of this butterfly weekly from August 1991 to May 1992. A total of 515 eggs found on 129 marked food plants were individually numbered and followed through larval instars until death or disappearance. Results suggest that egg predation and rainfall are the main factors responsible for the low level of first instar recruitment. Egg parasitism rate was considered high for a tropical insect population, although it accounted little for overall mortality. A vertical life table constructed with data from one generation showed mortality was similar among larval instars, but was significantly higher for the eggs. No larval parasitism was observed, a finding perhaps related to low larval densities at the site.

**KEY WORDS:** abundance; *Anaea ryphea*; life table; regulation; parasitism; tropics.

## INTRODUCTION

One of the most interesting issues in Population Ecology involves the mechanisms responsible for keeping population densities within certain limits, below their theoretical carrying capacities, as predicted by exponential models. Many factors can act together to reduce levels of reproduction and survivorship when density increases. The effect is said to be density-dependent, and these factors are said to be the population regulators (Lack 1954; Solomon 1964; Begon and Mortimer 1986) — although Wolda (1989b) states that there are no studies showing that density dependent processes definitely do act on natural populations in such a way as to keep numbers within stable limits.

It was believed that tropical insect populations should be less variable in numbers than those of temperate areas, both seasonally and between years (Andrewartha and Birch 1954; Solomon 1964; Pianka 1970), due to the assumed stability of tropical environments. Studies carried out later showed that tropical insect populations not only can be very stable in numbers (Ehrlich and Gilbert 1973) but some times are subject to fluctuations, outbreaks and variations in abundance similar to those that occur in temperate areas (Wolda and Foster 1978; Wolda 1983, 1989a; 1992 a,b). Even in tropical environments considered to be aseasonal, there is seasonality in insect phenology (McElravy *et al*. 1982; Wolda and

Flowers 1985), and one wonders what factors could be responsible for this phenomenon. It is known that, among others, thermoperiodism can influence growth rates (Beck 1983) and that photoperiodism plays an important role in the reproductive diapause of certain species of butterflies (Riley 1988), sometimes causing seasonality in their adult occurrence pattern.

Studies involving population variations in tropical insects, apart from analyzing reproduction, are also very concerned with mortality levels. Life tables are constructed to evaluate these parameters (Royama 1981; Stiling 1988; Hassell *et al.* 1989). Climatic and environmental factors, natural enemies, and competition are usually considered the main sources of mortality, but Crawley (1989) pointed out that outbreaks of herbivorous insects occurring soon after the use of broad spectrum insecticides suggest that their populations, when in low densities, are regulated by natural enemies alone. Natural enemies and competition for common resources are usually regulating factors, related to density (Nicholson 1933; Lack 1954; Eberhardt 1970; Lance *et al.* 1987).

Because there are very few studies that analyze mortality factors in natural tropical insect populations, especially in folivorous species, the aim of this study was to characterize the main sources of mortality acting on immature stages of the butterfly *Anaea ryphea* Cramer 1775 (Nymphalidae: Charaxinae) in Panama, including comments on its life cycle.

## Procedures
### Study site

The study site was a small forested area along the road leading to Galeta Island, Colón Province, on the Caribbean (north) coast of the Republic of Panama, east of the Panama Canal. The site is located at sea level, and the annual average temperature is around 28°C. Average rainfall at Galeta Island is 2,500 mm, the same value registered for Barro Colorado Island, which is located close by to the south. A dry season occurs, usually from December through April. The study area was chosen because it had 129 individuals of *Croton billbergianus* (Euphorbiaceae), the main larval foodplant of *A. ryphea* in Panama (personal observation). This number was considered suitable for my study.

### Data collection

I labelled all 129 plants with plastic tags, and made a weekly census from August 1991 to May 1992. Every leaf of each plant was checked, and eggs were numbered individually with a plastic band tied to the petiole of the leaf on which each was found. This method enabled me to identify each one of them, because there is usually but one egg or larva per leaf (Caldas 1994). I followed all of them until disappearance or death, and, depending upon age class, attributed different sources of mortality to each one. Predation was considered a source of mortality when no other

apparent reason could be found, as is usually done in studies of this kind. Rainfall was not included as a source of egg mortality because eggs were not washed away after strong storms (personal observation). When egg frequency increased I began to visit the area at shorter intervals, and by November I was going there almost every other day.

In addition to field observations, 40 eggs were taken to the laboratory and reared under constant temperature (16-18° C) and relative humidity (60-65%), in order to obtain information on life cycle.

## RESULTS AND DISCUSSION

Variation in abundance of *A. ryphea* larvae is shown in Figure 1. The pattern observed in the figure suggests that there was only one generation of significant size in the area during the study. *A. ryphea* larvae were not observed until early August, well after the beginning of the rainy season (late April). A significant number of eggs (n>5) was reached only in October. From then on, the larval population increased without a clear peak, and the number of individuals remained around thirty. In mid-December, when the population was decreasing, most of the plants were partially cut, without warning, in a road-side cleaning operation by the US Navy, and from then on no new larvae or eggs were found on the remaining leaves.

Rainfall was relatively constant, high and regular, between August and November, decreasing from December on, when dry season began. Rainfall was low throughout the rest of the study. Figure 2 shows a climograph for the area with a hypothetic constant temperature of 28°C — no temperature data were available due to equipment problems, but judging from data taken at La Galeta in previous years (Cubit *et al.* 1988) temperature at that area hardly varies. The main seasonality factor seems to be rainfall, which was unusually low during December 1991 and January/February 1992 (Windsor *et al.* 1990; D. Windsor, personal communication).

Rainfall pattern probably had a great influence on this population. I observed that strong rains kill young (mainly first instar, a few second instar) larvae (Caldas 1994). They also probably hinder oviposition (Ehrlich 1984). Recruitment of first instars was very low, in spite of continuous oviposition, because newly eclosed larvae were washed away easily from their perches on the midvein. Because rains were very strong and frequent (almost daily) at the site, this factor probably was very important in determining population numbers. Toward the end of the rainy season — in October, when rainfall subsided a little — the population was able to increase, but not very much, because strong rains began again. The population was thus prevented from reaching a peak until the abrupt start of dry season in December, at which time the bushes were cut. These two factors could have determined the end of the reproductive season, and population declined.

Of the 515 eggs marked, 85% disappeared, and parasitism by
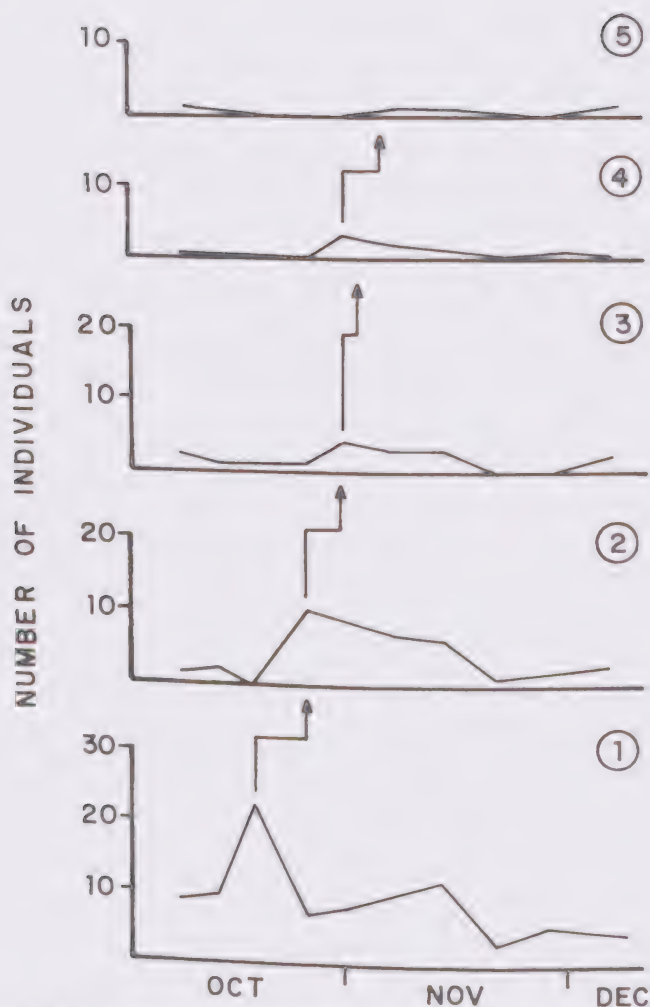
Figure 1. Total number of *Anaea ryphea* larvae (per instar) censused in Panama during the period of study. Arrows show the advance of a cohort through time.

*Trichogramma* sp. (Trichogrammatidae) was registered in 28% of the ones that remained in the field (Table 1). The evaluation of parasitism as a mortality factor can be particularly difficult if hosts cannot be identified individually (Hassell and Waage 1984). Overestimation of parasitism levels is common, because the remains of attacked individuals persist longer in the population. In this study all hosts were individually numbered, thus avoiding overestimation of egg parasitism. Still, the percentage found is considered high for a insect population. Courtney
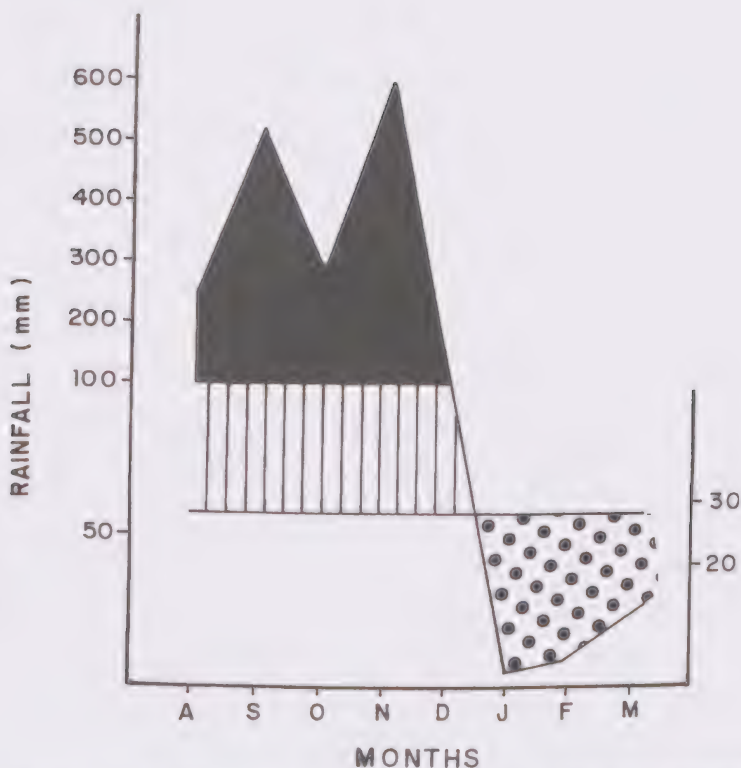
Figure 2. Climograph for the period of study in Panama; temperature is hypothetical (see text for details). Dotted area, dry period; lines, wet period; black, super-wet period.

and Duggan (1983) considered egg parasitism an important source of mortality, but pointed to the number of eggs laid by females as the key-factor for *Anthocaris cardamines* (Lepidoptera: Pieridae). Warren *et al.* (1986) say that egg parasitism by trichogrammatid wasps was always below 20% during their 5 years of study of *Leptidea sinapis* (Lepidoptera: Pieridae); the same thing happened with *Ladoga camilla* (Lepidoptera: Nymphalidae) in England (Pollard 1979). No density dependence was found in his study, although weather conditions were considered determinants of density. In a population of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in Australia, parasitism was considered insignificant compared to predation on eggs over sixteen generations (Danthanarayana 1983), a situation which seems to be similar to the one found for *A. ryphea* during this season in Panama. The high rate of egg disappearance attributed to predation seemed to have a much stronger impact on the *A. ryphea* population than did parasitism. The percentage of egg parasitism was even higher for the eggs reared in the laboratory (see below), although the low number of eggs in the rearing experiment

Table 1. *Anaea ryphea* egg survivorship in Panama (actual values; * = total k value for eggs).

| Total(N) | "Dead" | Mortality Factor | log N | k |
|---|---|---|---|---|
| 515 | | | 2.711 | |
| | 437 | disappearing | | 0.819 |
| 78 | | | 1.892 | |
| | 22 | parasitism | | 0.144 |
| 56 | | | 1.748 | |
| | 5 | non fertile | | 0.041 |
| 51 | | | 1.707 | |
| | | | | 1.004* |

Table 2. Vertical life table for *Anaea ryphea* during the period of study in Panama (* = total value for k; 1S, first instar; 2S, second instar; etc.).

| X | Total(N) | "dead" | Main Mortality Factor | $\log N_x$ | $k_x$ |
|---|---|---|---|---|---|
| Egg | 515 | | | 2.711 | |
| | | 422 | multiple | | 0.743 |
| 1S | 93 | | | 1.968 | |
| | | 52 | Rainfall | | 0.355 |
| 2S | 41 | | | 1.613 | |
| | | 24 | Predation/rainfall | | 0.383 |
| 3S | 17 | | | 1.230 | |
| | | 9 | Predation | | 0.327 |
| 4S | 8 | | | 0.903 | |
| | | 4 | Predation | | 0.301 |
| 5S | 4 | | | 0.602 | |
| | | | | | 2.109* |

does not allow it to be conclusive. The low density of larvae at the study site might be responsible for the apparent absence of larval parasitoids.

The life table shows high mortality for all instars (Table 2), although different sources are likely to be acting on each one of them. Thus, apart from parasitism and predation on eggs, predation by invertebrates (mainly ants and wasps) could be high for small larvae. Predation by vertebrates could be an important mortality factor also for large larvae, although the effect of rainfall cannot be discarded. The fact that mortality of *A. ryphea* third and fourth instars by rainfall has not been largely observed in the field at Campinas during 3 years of study (Caldas 1994) leads me to infer predation as the main mortality factor for these instars in Panama. Predators should be extremely efficient at predating *A. ryphea* larvae and eggs — hence the attribution of "predation" as the main mortality factor for third and fourth instars in the life table. No other explanation for the disappearance could be found, and it is common

to attribute it to predation, because it is very difficult to observe in the field (Pollard 1979; Courtney and Duggan 1983).

Two species of Ponerinae ants were observed frequently; one of them was described as interacting with Riodinidae larvae (DeVries 1988, 1991; DeVries and Baker 1989). Possibly these ants or other insects attracted to the extrafloral nectaries of *C. billbergianus* could be predators on larvae, or could be defending the plants against herbivory in the same way described by Tilman (1978) in cherry plants. This kind of interaction is not uncommon, and its role on herbivory reduction has been analyzed in various ways (Bentley 1976; Oliveira *et al.* 1987).

Fifteen (37.5%) of the forty eggs taken to the laboratory were parasitized by *Trichogramma* sp., and 2 were non-fertile. First instar larvae eclosed from the remaining 23 eggs 5 to 6 days later. Under constant conditions, the average time for the life cycle to be completed was 83.7 days (standard deviation 8.8 days). Individuals were smaller than the ones found in the field, and had the following characteristics:

First instar: maximum length 5 mm, first stadium average duration: 9 days (n=18).

Second instar: maximum length 9 mm, second stadium average duration: 7 days (n=17).

Third instar: maximum length 15 mm, third stadium average duration: 9 days (n=15).

Fourth instar: maximum length 19 mm, fourth stadium average duration: 13 days (n=14).

Fifth instar: maximum length 29 mm, fifth stadium average duration: 23 days (n=13).

Pre-pupa: maximum diameter 14 mm, prepupal average duration: 2.5 days (n=13).

Pupa: maximum length 13 mm, maximum width 10 mm, pupation average duration: 20 days (n=10).

The life cycle under these conditions is longer than the 50-60 days estimated for the same species in the field at Campinas, Brazil (Caldas 1994). Given that there is an inverse relationship between temperature and developing time for insects (Southwood 1978), it is likely that the rearing temperature (8-10°C under the average outdoor temperature) was responsible for the longer development times. The sex-ratio was 2:1 (15 females to 8 males), not significantly different from unity.

Considering that *A. ryphea* is a tropical butterfly with a probable seasonal pattern of appearance at Galeta, the question remains whether the low density observed could be considered the "lower limit" for this species. It seems reasonable to think that the ready availability of food (the food plants remain in the area after the road cleaning operation, but population did not increase again), together with climatic conditions, would favor an increase of this population, were there not mortality and immigration. The high oviposition rate observed at the site during the short period of study is a good sign of the response of females to this

conjunction of factors. I suspect that both the amplitude and seasonality of abundance of *A. ryphea* change over the years as has been observed in other insect species of nearby areas (Wolda 1992b). Predation on eggs and mechanical mortality of first instar larvae, in extremely heavy rains, could act together in a density independent way to prevent a higher level of recruitment. In any case, it could hardly be said that stable limits exist for the maintenance of this species in those areas, or that there is any sort of regulating mechanism acting in a density dependent way. As for this tropical area having environmental stability, it could be said that, apart from almost constant temperature, one cannot identify anything stable except predictably heavy rainfall. Catastrophic mortality is likely to occur everyday, but can this be considered a sign of stability? Not likely, given that the level of mortality caused by rainfall is not deterministic; it depends on a series of circumstantial factors, such as the position of the larva, the position of the leaf on which the larva is resting, the location of the plant itself, and so on.

## LITERATURE CITED

ANDREWARTHA, H.G. & L.C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago.

BECK, S.D. 1983. Insect thermoperiodism. Ann. Rev. Entomol. 28: 91-108.

BEGON, M. & M. MORTIMER. 1986. Population Ecology: a unified study of animals and plants. Blackwell, Oxford.

BENTLEY, B.L. 1976. Plants bearing extrafloral nectaries and associated ant community: Interhabitat differences in the reduction of herbivore damage. Ecology 57: 815-820.

CALDAS, A. 1994. Biology of *Anaea ryphea* (Nymphalidae) in Campinas, Brazil. J. Lepid. Soc. 48(3) (in press)

COURTNEY, S.P. & A.E. DUGGAN. 1983. The population biology of the Orange Tip butterfly *Anthocaris cardamines* in Britain. Ecol. Entomol. 8: 271-281.

CRAWLEY, M.J. 1989. Insect herbivores and plant population dynamics. Ann. Rev. Entomol. 34: 531-564.

CUBIT, J.D.; R.C. THOMPSON; H.M. CAFFEY; & D.M. WINDSOR. 1988. Hydrographic and Meteorological Studies of a Caribbean Fringing Reef at Punta Galeta, Panama: Hourly and Daily Variations for 1977-1985. Smithsonian Institution Press, Washington, D.C.

DANTHANARAYANA, W. 1983. Population ecology of the light brown apple moth, *Epyphias postvittana* (Lepidoptera: Tortricidae). J. Anim. Ecol. 52: 1-33.

DEVRIES, P.J. 1988. The larval ant organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. Zool. J. Linn. Soc. 94: 379-393.

—— 1991. Mutualism between *Thisbe irenea* butterflies and ants, and the role

of ant ecology in the evolution of larval-ant associations. Biol. J. Linn. Soc. 43: 179-195.

DeVries, P.J. & I. Baker. 1989. Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. J. New York Entomol. Soc. 97: 332-340.

Eberhardt, L.L. 1970. Correlation, regression and density dependence. Ecology 51: 306-310.

Ehrlich, P.R. 1984. The structure and dynamics of butterfly populations. 25-40. In R.I. Vane-Wright and P.R. Ackery (eds) The biology of butterflies. Academic Press, London.

Ehrlich, P.R. & L.E. Gilbert. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5: 69-82.

Hassel, M.P., J. Latto & R.M. May. 1989. Seeing the wood for the trees: detecting density-dependence from existing life-table studies. J. Anim. Ecol. 58: 883-892.

Hassel, M.P. & J.K. Waage. 1984. Host-parasitoid population interactions. Ann. Rev. Entomol. 29: 89-114.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.

Lance, D.R., J.S. Elkinton & C.P. Schwalbe. 1987. Behaviour of late-instar gypsy moth larvae in high and low density populations. Ecol. Entomol. 12: 267-273.

McElravy, E.P., H. Wolda & V.H. Resh. 1982. Seasonality and annual variability of caddisfly adults (Trichoptera) in a "non-seasonal" tropical environment. Archiv. fur Hydrobiologie 94: 302-317.

Nicholson, A.J. 1933. The balance of animal populations. J. Anim. Ecol. 2: 132-178.

Oliveira, P.S., A.F. da Silva & A.B. Martins. 1987. Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential anti-herbivore agents. Oecologia 74: 228-230.

Pianka, E.R. 1970. On r- and k-selection. Am. Nat. 104: 592-197.

Pollard, E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga camilla* in England. Ecol. Entomol. 4: 61-74.

Riley, T.J. 1988. Effect of larval photoperiod on mating and reproductive diapause in seasonal forms of *Anaea andria* (Nymphalidae). J. Lepid. Soc. 42: 263-268.

Royama, T. 1981. Evaluation of mortality factors in insect life table analysis. Ecol. Monographs 51: 495-505.

Solomon, M.E. 1964. Analysis of processes involved in the natural control of insects. Adv. Ecol. Res. 2: 1-58.

Southwood, T.R.E. 1978. Ecological methods with particular reference to the study of insect populations. Chapman and Hall, New York.

Stiling, P. 1988. Density-dependent processes and key factors in insect populations. J. Anim. Ecol. 57: 581-593.

Tilman, D. 1978. Cherries, ants and tent caterpillars: Timing of nectar production in relation to susceptibility of caterpillars to ant predation. Ecology 59: 686-692.

Warren, M.S., E. Pollard & T.J. Bibby. 1986. Annual and long-term changes in a population of the wood white butterfly *Leptidea sinapis*. J. Anim. Ecol. 55: 707-719.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: Long-

term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, DC.

WOLDA, H. 1983. "Long-term" stability of tropical insect populations. Res. Popul. Ecol. Suppl. 3: 112-126.

—— 1989a. Seasonal cues in tropical organisms. Rainfall? Not necessarily! Oecologia 80: 437-442.

—— 1989b. The equilibrium concept and density dependence tests. What does it all mean? Oecologia 81: 430-432.

—— 1992a. Stability of environment and of insect populations. Res. Popul. Ecol. 34: 213-225.

—— 1992b. Trends in abundance of tropical forest insects. Oecologia 89: 47-52.

WOLDA, H. & R.W. FLOWERS. 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a "nonseasonal" tropical environment. Biotropica 17: 330-335.

WOLDA, H. & R. FOSTER. 1978. *Zunacetha annulata* (Lep.: Dioptidae), an outbreak insect in a neotropical forest. Geo-Eco-Trop. 2: 443-454.

# Turnover of some biochemical constituents during embryogenesis of *Antheraea mylitta* Drury to monitor the efficacy of carbendazim and chloroquine in controlling microsporidiosis

P.P. Srivastava, N.D. Banerjee, N.N. Saxena, R.M. Shukla, A.K. Bansal and K. Thangavelu

Central Tasar Research and Training Institute, P.O. Piska Nagri, Ranchi - 835303, Bihar, India

**Abstract.** The microsporidian *Nosema* sp. is a major pathogen of the tropical tasar silkworm, *Antheraea mylitta* Drury. In acute condition, the disease affects moth emergence, reproductive potential, egg and larval viability, and cocoon characters. Efficacy of 0.005% carbendazim (a systemic fungicide) and 0.50% chloroquine (an anti- protozoan drug) on the virulence of *Nosema* sp. was investigated through studies of the 24-hourly turnover of total proteins, total carbohydrates, total lipids and total free amino acids during embryogenesis of *A. mylitta*. Results of this experiment indicate that chloroquine appeared less deleterious to *Nosema* sp. in comparison to carbendazim which was found to be significantly effective in restoring the level of all four biochemical constituents. Also, the effectiveness of carbendazim was reflected in a significant improvement of the effective rate of rearing and silk ratio while chloroquine was least effective.

## INTRODUCTION

Microsporidians are generally considered a most important group of protozoan parasites infecting insects (McLaughlin, 1971). Pebrine, caused by the microsporidian, *Nosema* sp., is an important mortality factor of tasar silkworm, *Antheraea mylitta* Drury . It has threatened both tasar culture and tasar seed production. The pathogen is transmitted both horizontally and vertically in the population and multiplies rapidly (Jolly & Sen, 1972). Further, outdoor rearing of tasar silkworm enhances the possibility of the pathogen being disseminated through common vectors, making it extremely difficult to eradicate the disease. Various attempts have been made to suppress the microsporidian infection in insects (Allen & Brunson, 1949; Katznelson & Jamieson, 1952; Bailey, 1953; Jamieson, 1955; Fox & Weiser, 1959; Weiser, 1961; Moffett *et al.*, 1969; Lynch & Lewis, 1971; Wilson, 1974; Hamm *et al.* 1977; Xian, 1987), but a suitable therapy has not yet been discovered.

Effectiveness of fungicides to control the disease has been investigated by several workers (Flint *et al.*, 1972; Hsiao & Hsiao, 1973; Armstrong,

1976; Harvey & Gaudet, 1977; Brooks *et al.*, 1978 and Griyaghey *et al.*, 1987). Chloroquine, mainly an antimalarial drug, was found effective against other protozoan infection such as *Trypanosoma* (Otigbuo & Patrick, 1988). Consequently the present study was undertaken to test various doses of a systemic fungicide, carbendazim, { 2(Methoxy - carbomylamino)Benzimidazole} and an antiprotozoan drug, chloroquine. Efficacy of carbendazim and chloroquine was monitored throughout embryogenesis by measuring 24-hourly turnover of proteins, carbohy-drates, lipids and free amino acids. These biochemical constituents were reported to decrease in eggs following infection (Sinha *et al.*, 1988 and Sinha *et al.*, *1991* ).

## Materials and Methods

Larval stages were treated with drugs during rearing. Assay larvae were reared in four batches with *Terminalia arjuna* as host plant. The first batch comprised of healthy larvae (uninfected control) was reared in a separate field to avoid secondary contamination. The other three batches were pebrine infected and comprised an infected control, carbendazim treated and chloroquine treated. These larvae were reared at different locations in one field. The third and fourth batches were treated with 4 concentrations of carbendazim (0.005, 0.01, 0.02 and 0.04%) and 3 concentrations of chloroquine (0.01, 0.1 and 0.5%) respectively. The doses were selected on the basis of exploratory trials in previous years. Drug administration was by foliar spray of an aqueous solution using a Knapsack sprayer.

Carbendazim was fed continuously to the larvae from II stage onward until the cocoon was spun. Chloroquine was fed for 3 days to II and III stage larvae respectively. Five replicates of 200 larvae each were initially taken per batch for all treatments. The mortality of larvae was recorded regularly and the data were statistically analyzed.

The treatment which showed the best rearing performance, 0.005% carbendazim (CB) and 0.50% of chloroquine (CQ), was chosen for the biochemi-cal assays throughout embryogenesis at 24-hour intervals. Four biochemical constituents, viz. total proteins, total carbohydrates, total lipids and total free amino acids were assayed by the methods of Lowry *et al.* (1951), Dubois *et al.* (1956), van Handel (1985) and Moore and Stein (1948) respectively.

## Results and Discussion

Data presented in Table1 indicate rearing performance of carbendazim (CB) and chloroquine (CQ) in controlling the micosporidiosis. It is evident that CB at 0.005% is significantly ($P < 0.05$) effective in increas-ing survivability (ERR) and silk ratio in comparison to the infected, but untreated control set. Increasing CB concentration does not signifi-cantly decrease larval mortality due to pebrine. However, the economic characters of ERR & silk ratio decrease significantly. The data suggest a side effect of higher doses of CB on the larvae of A. *mylitta*. The effect of 0.50% CQ is superior to other doses of this drug for ERR and silk ratio. However, when performance of both the drugs are compared vis-a-vis economic yield, CB has an edge over CQ.

Table 1. Rearing performances of carbendazim and chloroquine in controlling the microspordiosis.

| Drug | Concentration (%) | LMM (%) | ERR (%) | Cocoon Characters | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | | | C.W. (g) | S.W. (g) | Silk Ratio (%) |
| Carbendazim | 0. 005 | 31.10 | 45. 60 | 10. 80 | 1.29 | 11.94 |
| | 0. 010 | 28.20 | 27. 00 | 11. 00 | 1.15 | 10.41 |
| | 0. 020 | 27.60 | 28.60 | 10.47 | 0.88 | 8.36 |
| | 0. 040 | 26.60 | 26. 50 | 11.21 | 1.29 | 11.50 |
| Infected control | | 60.00 | 19. 50 | 10.89 | 1.10 | 10.08 |
| CD at 5% | | 4.114 | 15.333 | 1.072 | 0.223 | 1.587 |
| Chloroquine | 0.010 | 38.10 | 27.90 | 11.29 | 1.28 | 11.36 |
| | 0.100 | 34.80 | 24.80 | 11.20 | 1.21 | 10.83 |
| | 0.500 | 31.00 | 30.10 | 11.20 | 1.31 | 11.72 |
| Infected control | | 60.00 | 19.50 | 10.89 | 1.10 | 10.08 |
| CD at 5% | | 5.982 | 7.677 | 0.477 | 0.157 | 1.239 |
| Healthy control | | 0.00 | 47.20 | 12.24 | 1.32 | 10.75 |
| Pooled CD at 5% | | 13.071 | 17.388 | 0.670 | 0.205 | 1.735 |

LMM - Larval mortality due to microsporidiosis; ERR - Effective rate of rearing; C. W. - Cocoon weight; S. W. - Shell weight .
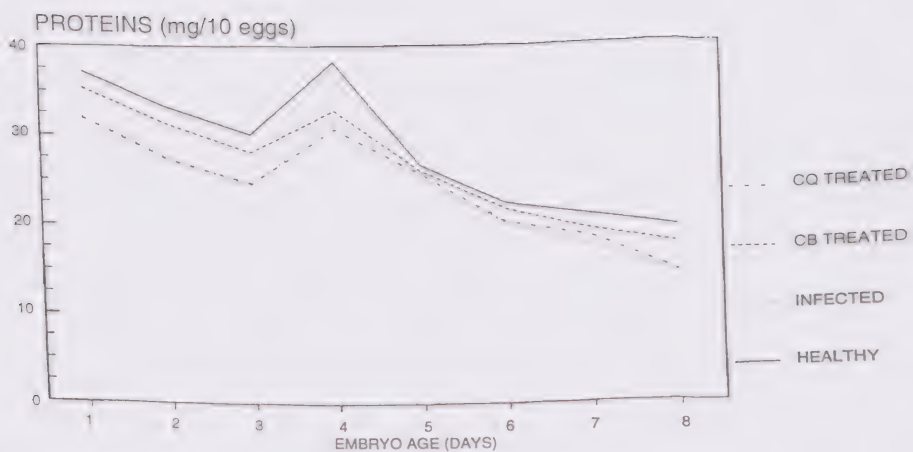
## Biochemical monitoring

Daily changes in healthy, pebrine infected, CB (0.005%) treated and CQ (0.50%) treated eggs of A. *mylitta* with regard to total proteins, total carbohydrates, total lipids and total free amino acids are given in Figures 1a, b, c & d respectively. The data were recorded at 24-hour intervals and during the complete period of embryogenesis until hatching . Figures 1a to 1d reveal that all four biochemical parameters show an almost uniform pattern of rise and depression with respect to all treatments: healthy, infected, CB treated and CQ treated. The data obtained during embryogenesis are pooled and presented in Table II.
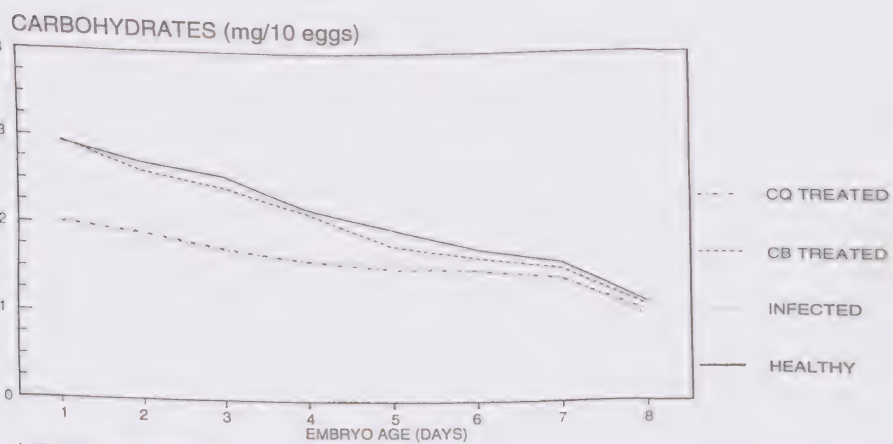
## Total Proteins

As evident from Fig. 1a, the concentration of proteins in all four treatments decreases from the first to the third day of embryogenesis and then increases on fourth day, finally decreasing until the larvae hatch. Rise and fall in protein level during embryonic development suggest both breakdown and synthesis of organ specific proteins occur-
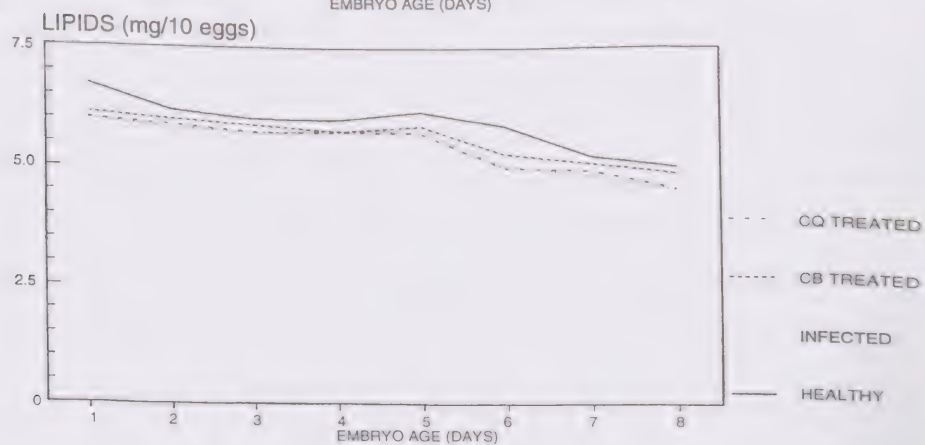
A

PROTEINS (mg/10 eggs)

CQ TREATED

CB TREATED

INFECTED

HEALTHY

EMBRYO AGE (DAYS)

B CARBOHYDRATES (mg/10 eggs)

CQ TREATED

CB TREATED

INFECTED

HEALTHY

EMBRYO AGE (DAYS)

C LIPIDS (mg/10 eggs)

CQ TREATED

CB TREATED

INFECTED

HEALTHY
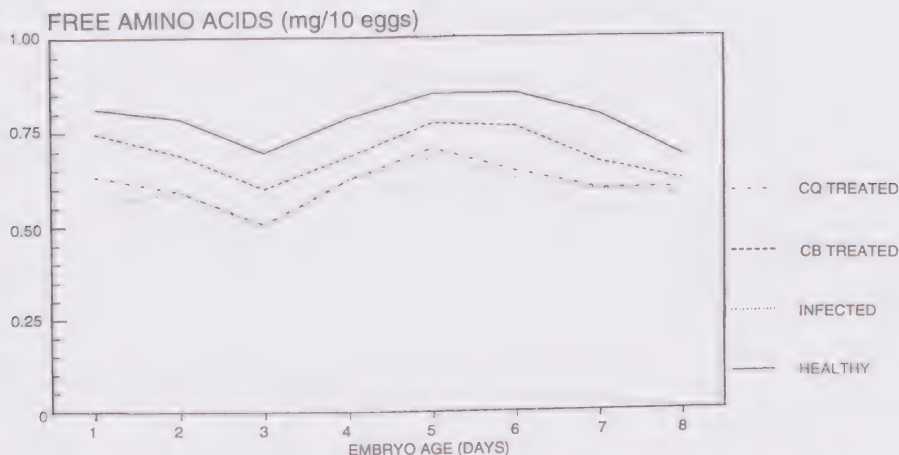
EMBRYO AGE (DAYS)

D



FREE AMINO ACIDS (mg/10 eggs)

Fig. 1. Showing 24-hourly turnover in the concentrations (mg/10 eggs) of bio-
chemical contituents during embryogenesis of A. mylitta D. with respect to
four treatments viz. healthy, infected, carbendazim (CB) and chloroquine
(CQ).
a. Changes in the concentration of total proteins
b. Changes in the concentration of total carbohydrates.
c. Changes in the concentration of total lipids.
d. Changes in the concentration of total free amino acids.

ring simultaneously (Sinha *et al.*, 1991). The data of Table 2 indicate
that CQ has no effect while CB is significantly ($P < 0.05$) effective in
improving the protein level in comparison to infected animals.

**Total Carbohydrates**

Total carbohydrates show a gradual decrease in concentration during
the course of embryogenesis in all the four treatments (Fig. 1b). Urbani
and Bellini (1959) observed a gradual decrease in carbohydrates for
energy requirements during embryogenesis of silkworm *Bombyx mori*.
Sinha *et al.* .(1991) reported similar trends of turnover in healthy and
pebrine infected eggs of *A. mylitta* during embryogenesis. Table 2
indicates that CB treatment significantly restores the level of carbohy-
drates of infected embryos while CQ has no effect.

**Total Lipids**

Fig. 1c shows that total lipids also fall gradually from first day till the
termination of embryogenesis, except for a slight rise on day 5. Our
study corroborates the report of Goel *et al.* (1988) for the developing
healthy embryos of *A. mylitta*. Table 2 shows that CB has significant ($P < 0.05$) impact on restoring lipid levels in comparison to the values of
infected eggs. CQ was again ineffective.

Table 2. Effect of carbendazim (CB) and chloroquine (CQ) on pooled values of total proteins, total carbohydrates, total lipids and total free amino acids in the eggs (Mean ± Standard Error)

| Treatments | Biochemical Constituents (mg/10 eggs) | | | |
|---|---|---|---|---|
| | Total Proteins | Total Carbohydrates | Total Lipids | Total Free Amino Acids |
| Healthy | 28.525 ± 1.428 | 2.111 ± 0.120 | 5.894 ± 0.108 | 0.780 ± 0.012 |
| Infected | 24.067 ± 1.258 | 1.590 ± 0.062 | 5.431 ± 0.108 | 0.594 ± 0.011 |
| CB treated | 26.513 ± 1.278 | 2.027 ± 0.121 | 5.600 ± 0.092 | 0.693 ± 0.013 |
| CQ treated | 24.175 ± 1.187 | 1.591 ± 0.060 | 5.437 ± 1.106 | 0.613 ± 0.012 |
| CD at 5% | 0.234 | 0.018 | 0.013 | 0.006 |

## Total Free Amino Acids

Figure 1d shows the turnover of free amino acids during the embryogenesis for all the four treatments. The trend of change in free amino acids content in healthy and infected eggs confirm the observations of Sinha *et al.* (1988) in *A. mylitta.* The data of Table 2 indicate that CQ correlates with CB to significantly (P< 0.05) increase the concentration of total free amino acids in infected eggs. The efficacy of chloroquine may be attributed to its retardation of protein synthesis in protozoa (Vial *et al., 1988*), thereby raising the free amino acid pool.

The results of this study suggest that 0.005% carbendazim treatment of larval stages during rearing has a definite effect in suppressing the development of *Nosema* sp. in *A. mylitta* while 0.50% chloroquine has the least effect. Hsiao & Hsiao (1973) demonstrated that Benomyl, another systemic fungicide, is an antimicrosporidian agent on a *Nosema* sp. in the alfalfa weevil. In fact, Benomyl containing diets fed to parasitized weevils for three days completely eliminated the *Nosema* parasite. Shinholster (1974), Armstrong (1976) and Harvey & Gaudet (1977) also observed the effectiveness of Benomyl against microsporidian infection. Griyaghey *et al.* (1987) experimented with treating eggs and larvae of *A. mylitta* with 2% Bengard (a systemic fungicide ) and observed decreased concentrations of spores in infected larvae. This ultimately increased the vigor and viability of larvae and produced higher yields and silk content. All these findings concur with our present results. Thus the biochemical parameters employed in our study may be useful as tools to monitor the efficacy of other drugs. In order to understand the mode of action of these drugs with the biochemical constituents, further experiments are necessary.

## LITERATURE CITED

ALLEN, H. W. & M. H. BRUNSON, 1949. Control of *Nosema* disease of potato tuber worm, a host used in the mass production of *Microcentreus ancylivorus*. Science 105:394.

ARMSTRONG, E., 1976. Fumidil B and Benomyl:chemical control of *Nosema kingi* in *Drosophila willistoni*. J. Invertebr. Pathol. 27:363-366.

BAILEY, L., 1953. Effects of Fumagillin upon *Nosema apis*. Nature 171:212-213.

BROOKS, W. M., J. D. CRANFORD & L. W. PEARCE, 1978. Bemnomyl: effectiveness against the microsporidian *Nosema heliothidis* in the corn earworm *Heliothis zea*. J. Inverteber. Pathol. 31:239-245.

DUBOIS, M., K. A. GILLES, J. K. HAMILTON, P. A. REBERS & F. SMITH, 1956. Colorimeteric method for determination of sugars and related substances. Analyt. Chem. 28:350-355.

FLINT, H. M. , J. EATON & W. KLASSEN, 1972. Use of Fumidil B to reduce microsporidian disease in colonies of the boll weevil. Ann. Entomol. Soc. Amer. 65:942-945.

FOX, R. M. & J. WEISER, 1959. A microsporidian parasite of *Anopheles gambia* in Liberia. J. Parasitol. 45:21-30.

GOEL, R. K. A. K. SINHA & K. SENGUPTA, 1988. Changes in lipid contents during embryonic development of tasar silkworm, *Antheraea mylitta* Drury. Indian J. Seric. 27(1): 40-41.

GRIYAGHEY, U. P., K. SENGUPTA, P. KUMAR, RAM MURTI, A. K. SINHA& U. S. P. SINHA, 1987. Studies on the effectiveness of Bengard in controlling the microsporidian disease of *Antheraea mylitta* D. Sericologia 27(3) : 533-540.

HAMM, J. J., R. L. BURTON, J. R. YOUNG & R. T. DENIER, 1977. Elimination of *Nosema heliothidis* from a laboratory colony of corn earworm. Ann. Entomol. Soc. Amer. 64: 624-627.

HARVEY, G. T. & P. M. GAUDET, 1977. The effects of Benomyl on the incidence of microsporidia and the developmental performance of Eastern Spruce Bud worm (Lepidoptera : Tortricidae). Canad. Entomol 109 : 986-993.

HSIAO, T & C. HSIAO, 1973. Benomyl: a novel drug for controllig a microsporidian disease of the alfalfa weevil. J. Invertebr. Pathol. 22: 303-304.

JAMIESON, C. A., 1955. *Nosema* disease and its control with Fumagillin. Amer. Bee J. 94:52. Srivastava *et al*.

JOLLY, M. S. & S. K. SEN, 1972. Infection of *Antheraea mylitta* Drury (Lepidoptera : Saturniidae) by a microsporidian (*Nosema* sp. ). Indian J. Seric. 11(1): 52-57.

KATZNELSON, H. & C. A. JAMIESON, 1952. Control of *Nosema* disease of honeybee with Fumagillin. Science 115: 70-71.

LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR & R. J. RANDALL, 1951. Protein measurents with folin phenol reagent. J. Biol. Chem. 193: 265-275.

LYNCH, R. E. & L. C. LEWIS, 1971. Reoccurrence of the microsporidian *Perezia pyraustae* in the european corn borer, *Ostrinia nubilalis*, reared on diet containing Fumidil B. J. Invertebr. Pathol. 17(2) : 243-246.

MCLAUGHLIN, R., 1971. Use of protozoans for microbial control in insects, In"Microbial Control of Insects and Mites"(H. D. Burgers and N. W. Hussey, eds.), pp. 151-172. Acadamic Press, New York.

MOFFETT, J. O., J. J. LACKETT & J. D. HITCHCOCK. 1969. Compounds tested for control of *Nosema* in housebees. J. Econ. Entomol. 62(4) : 886-889.

MOORE, S. & W. H. STEIN, 1948. Photometric ninhydrine method for use in the chromatography of amino acids. J. Biol. Chem. 176: 367-388.

OTIGBUO, I. N. & T. K. W. PATRICK, 1988. The *in vitro* and *in vivo* effects of metromidazole and chloroquine on *Trypanosoma brucci brucci*. J. Parasitol. 74(2); 201-206.

SHINHOLSTER, D. L., 1974. The effect of X-irradiation and chemotherapy on the host-parasite relationship between *Tribolium castaneum* (Herbst.) and two protozoan parasites, *Nosema whitei* Weiser and *Adelina tribolii* Hesse. PhD Thesis, Cornell Universirty, Ithacha, New York.

SINHA, A. K., U. S. P. SINHA & K. SENGUPTA, 1988. Changes in free amino acids in developing pebrinised embryo of *Antheraea mylitta* Drury. Indian J. Seric. 27(2): 109-112.

SINHA, U. S. P., A. K. SINHA & S. S. SINHA, 1991. Changes in concentration of ptoteins and carbohydrates in the developing healthy and pebrine infected embryoes of tropical tasar silkworm, *Antheraea mylitta* D. Indian J. Seric. 30(2); 155-156.

URBANI, E. & L. BELLINI, 1959. Total nitrogen, carbohydrates, and fat in the embryonal development of *Bombyx mori*. Ricerca. Sci. 29 (8) : 1725-1730.

VAN HANDEL, E., 1985. Rapid determination of total lipids in mosquitoes. J. Am. Mosq. Control Assoc. 1(3): 302-304.

VIAL, H. J., M. L. ANCELIN, M. J. THUET & J. R. PHILIPPOT, 1988. Differential effects of chloroquine on the phospholipid metabolism of *Plasmodium* infected erthrocytes. Biochem. Pharmacol. 37(16): 3139-3148.

WEISER, J., 1961. Die mikrospridienals. Parasiten der insekten. Monograpg. Angew. Entomon. 17: 1-149.

WILSON, G. G., 1974. The use of Fumidil B to suppress the microsporidian *Nosema fumiferanae* in stock cultures of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canad. Entomol. 106: 995-996.

XIAN, L. S., 1987. The effect of chemotherapy on pebrine disease of *Bombyx mori*. Sericologia. 27(3): 405-410.

# The influence of larval age and ant number on myrmecophilous interactions of the African Grass Blue butterfly, *Zizeeria knysna* (Lepidoptera: Lycaenidae)

Konrad Fiedler and Dorthe Hagemann

Zoologie II, Biozentrum der Universität, Am Hubland, D-97074 Würzburg, Germany

**Abstract.** Interactions between myrmecophilous *Zizeeria knysna* larvae and *Lasius flavus* ants were quantitatively studied in laboratory experiments. Larvae delivered secretions from their dorsal nectar organ (DNO) more frequently in the initial 3-minute interval of an interaction than later on. Tentacle eversions were likewise more common at the beginning of interactions. Non-feeding prepupal larvae secreted significantly more droplets than feeding fourth instars. Actual tending levels differed between larvae tested with 5 (2.6-3.1 ants per larva) or 15 ants (5.3 ants/larva), respectively. Secretion rates increased with tending level (5-ant trials: feeding L4 larvae 5.5 DNO droplets/h, prepupae 16.4 droplets/h; 15-ant trials: feeding L4 9.5 droplets/h, prepupae 25.5 droplets/h). Secretion droplets averaged 0.2 mm in diameter (volume 0.004 µl). From these data, a model is developed to estimate lifetime DNO secretion amounts of individual larvae. Estimates range from 1.3-4.7 µl per larva in 5 d, representing approximately 0.2-0.7 mg carbohydrates with a physiological energy equivalent of 3.4-12 J. Hence, *Z. knysna* larvae provide only a marginal food reward for attendant ants, suggesting that myrmecophily is a low-cost life-history strategy in that butterfly species.

**KEY WORDS:** mutualism - symbiosis - caterpillars - strategic behavior - energetic investment - Formicidae - Lycaenidae

## INTRODUCTION

Interactions between immatures of butterflies and ants, termed myrmecophily, are widely known from a broad range of lycaenid and riodinid species (see reviews by Malicky 1969; Cottrell 1984; Pierce 1989; Fiedler 1991). Much work has concentrated on the description of individual life-cycles, on the structure and function of myrmecophilous organs, and on the ecological outcome of myrmecophily (mutualism, parasitism). In contrast, fewer studies have focused on detailed quantitative studies of the relevant behaviors. Such studies either attempted to quantify myrmecophilous interactions in the light of interspecific comparisons (Fiedler 1991, Ballmer & Pratt 1991), or they experimentally elucidated phenomena like the release of food recruitment in tending ants (Fiedler & Maschwitz 1989), the secretory capacity of individual larvae (Fiedler & Maschwitz 1988a), the influence of larval food on the

expression of myrmecophily (Fiedler 1990, Baylis & Pierce 1991), or on conditional factors regulating secretory behavior (Leimar & Axén 1993). With the exception of the last mentioned work, all studies assumed that secretion rates observed in experiments are more or less representative for the populations or species under investigation.

The energetic investment of lycaenid larvae in their symbiosis with ants may, however, be plastic in response to the actual needs. For example, Leimar & Axén (1993) showed that larvae of the facultatively myrmecophilous species *Polyommatus icarus* (Rottemburg, 1775) delivered more secretion droplets from their nectar organ when subjected to a simulated attack or when tended by two instead of one *Lasius flavus* (Fabricius, 1781) worker ants. Further increase in the number of tending ants did not add to secretion rates. In addition, the intensity of myrmecophily often increases with progressive larval development (e.g. Malicky 1969, Fiedler 1989), although Leimar & Axén (1993) observed no significant correlation between body mass and secretion rates among fourth instars of *P. icarus*. Wagner (1993) demonstrated significant weight losses in non-feeding prepupal larvae of a Nearctic facultative myrmecophile, *Hemiargus isola* (Reakirt, [1867]). Her result points to particularly intensive and energetically costly interactions with ants in the prepupal phase.

We here present a quantitative laboratory study on myrmecophilous interactions between larvae of *Zizeeria knsyna* (Trimen, 1862) and the ant *Lasius flavus*. Specifically, we address the following questions: 1) Are the secretions from the dorsal nectar organ (DNO) delivered at a constant rate or is there a temporal pattern in the secretory behavior? 2) Are the secretion rates of feeding mature larvae equal to those of non-feeding prepupal larvae? 3) Does the number of tending ants influence the outcome of larva-ant interactions? 4) Is larval myrmecophily correlated with body mass and how are the various myrmecophilous behaviors correlated with each other? 5) Finally, we try to estimate the lifetime investment in nectar-like secretions of individual larvae of *Z. knysna*.

## MATERIAL AND METHODS
### Study organisms

The African Grass Blue, *Zizeeria knysna* is a small butterfly distributed from the Canary islands and the Iberian Peninsula southwards throughout most of Africa, including Madagascar and the Mascarene islands, eastwards extending to Arabia. The species is polyvoltine. It occurs in open, xeric habitats, and the larvae feed on a variety of plants, notably various genera of Fabaceae, but also on members of Amaranthaceae, Chenopodiaceae, Oxalidaceae, Zygophyllaceae and Euphorbiaceae. In addition, oviposition has been observed on Malvaceae (Schurian 1994). There are 4 larval instars, with older larvae facultatively tended by ants (see Clark & Dickson 1971 for a detailed illustrated description of the basic life cycle). Tending ants have rarely been specified. Schurian (1994) recorded a *Pheidole* species (Myrmicinae) from the Canary islands. Further records, such as *Tapinoma melanocephalum* (Dolichoderinae: Warnecke 1932/

33), refer to the related butterfly, *Z. karsandra* (Moore, 1865), whose status as a distinct species has been subject to controversy until recently.

For our experiments, we used laboratory-bred offspring of females caught on Gran Canaria. Butterflies were kept in plastic cages in a greenhouse (see Schurian 1989, for details on the breeding method). The laboratory stock was maintained for 5 generations throughout the year 1993 using inflorescences and young foliage of *Medicago sativa* (Fabaceae) as the main larval food. Experiments were conducted with members of the 4th and 5th generation between September and November 1993. To control for possible effects of larval diet (Fiedler 1990, Baylis & Pierce 1991), we fed all experimental animals invariably with young foliage of *M. sativa*. Larvae were reared in an environmental chamber at 25.5 °C and 15:9 h L:D cycle. They were kept in transparent plastic vials (250 ml) lined with moist filter paper. *Ad libitum* amounts of freshly cut terminal foliage of *M. sativa* were provided daily, and the larvae were transferred to a new rearing vial every day to minimize the risk of diseases.

*Lasius flavus* (Formicinae) is a common subterranean ant species of the Palearctic region. It mostly occurs in open grassland or heaths, but also colonizes forests (Kutter 1977). *L. flavus* avoids truly xeric habitats and therefore probably rarely, if ever, co-occurs with *Z. knysna*, although the distributions of both species overlap on the Iberian Peninsula and in northwestern Africa. The diet of *L. flavus* ants mainly consists of the honeydew of root aphids. Furthermore, aphids are eaten in large quantities to obtain proteins (Pontin 1978). Due to their food specialization, *L. flavus* ants show intensive trophobiotic behavior even under laboratory conditions and avidly tend lycaenid larvae and pupae (e.g. Fiedler 1990, 1991, Leimar & Axén 1993). Therefore, this ant species is very suitable for laboratory studies on lycaenid myrmecophily, although associations between *L. flavus* worker ants and lycaenid immatures have rarely been observed in nature (Fiedler 1991).

Ant colonies were kept at laboratory temperatures of approx. 20-23 °C under ambient light conditions in large earth nests, which were maintained in plastic arenas (size 64 cm × 44 cm × 12 cm) with a bottom of plaster of Paris. Sidewalls were smeared with Fluon to prevent ants from escaping. The nests were sprayed daily with water to adjust humidity, and food (honey-water and cut cockroaches) was provided as needed. For our experiments we used three ant colonies originating from northern Bavaria.

## Experimental procedure

Experiments were conducted in plastic arenas (10 cm × 10 cm × 6 cm) with a bottom of plaster. The bottom was kept moist during all trials. For experiments, either 5 or 15 foraging workers of *L. flavus* were taken while on their way to a feeding place in the foraging area of the nest arenas and were carefully transferred into a test arena with the help of a brush. Disturbance of ants due to handling was minimized and another 5 min allowed before a single test larva was placed in the center of the test arena. After that time period the alarm behavior of the ants had subsided. Beginning with the first encounter between an ant and the larva, we recorded the behavioral interactions for 15 min. Observations were made under a Zeiss stereomicoscope at ten-fold magnification with normal daylight between 9:00 h and 15:00 h local time. The arena was rotated from time to time to eliminate possible effects of directional illumination on ant activity.

The following events were counted every 30 seconds: a) the number of ants in

immediate physical contact with the larva; b) the number of DNO secretion droplets delivered during that time interval; and c) the number of eversions of the tentacle organs (TOs). Total duration of contacts between ants and the test larva were recorded with a stop-watch to the nearest second. At the end of each experiment, the larva was weighed to the nearest 0.1 mg (Sartorius Basic BA 61 balance).

Each set of worker ants was used for a maximum of three subsequent experiments to avoid possible effects due to a drop in ant activity if kept in isolation from their nestmates for longer periods. In a large series of earlier experiments (Burghardt & Fiedler, unpubl.) we have established that no adverse effects occur if *L. flavus* are kept away from their colony for up to 1 h. At least 5 min elapsed between the experiments.

Two classes of larvae were used in experiments. "Feeding larvae" refers to animals that were well within the fourth (= final) instar and had not yet left the foodplant to settle down for pupation. Feeding L4 larvae in our tests ranged from 25.7-53.0 mg (wet weight) and were all near their larval peak body mass. "Non-feeding prepupal larvae" denotes those which had stopped feeding. Such larvae had mostly left the hostplant to settle down among the filter papers, but had not yet spun a silk girdle. They all showed a characteristic transformation of color: their markings became indistinct and the overall appearence was transparent and "glossy". Non-feeding prepupal larvae are still able to crawl and their myrmecophilous organs remain functional. Wet weights of non-feeding prepupae tested ranged from 26.1-51.2 mg. After one day, the true immobile girdled prepupa is formed, which is no longer able to evert the tentacle organs.

Larval sex discrimination was not attempted, since sexual weight dimorphism in our laboratory cultures was generally low. Any larva was tested only once per day and at most twice per lifetime (once as a feeding larva, again as a non-feeding prepupa). A few larvae in each series were examined in only one of these phases.

## Quantitative evaluation of results

Attractiveness, or actual tending level, was calculated from data recorded for each individual larva (defined as the arithmetic mean of the number of tending ants throughout the experiment, i.e. across 30 census points). In addition, we calculated the total number of secretion droplets delivered per experiment and the sum of tentacle eversions. To examine the time course of larva-ant interactions we subdivided each experimental period into five 3-min intervals. Since this analysis revealed a distinct difference between the first 3-min interval and the subsequent intervals (see below), we also calculated the number of secretion acts and tentacle eversions of each experimental larva for the final 12 min of a trial.

All data were then subjected to statistical analysis. Comparisons between the larval age classes or between the experimental series with different ant numbers were computed using the non-parametric U-test of Mann & Whitney, while comparisons between the time intervals within experiments were made using Wilcoxon's matched-pairs signed-ranks test. Spearman rank correlations between myrmecophily parameters and larval weight were likewise calculated (Sachs 1992).

## RESULTS
### Temporal patterns of larva-ant interactions

Regardless of larval age or ant number, all experiments with *Z. knysna*

larvae revealed similar temporal patterns of myrmecophilous behaviors and interactions. DNO secretions occurred significantly more often in the first 3-min interval than in the four subsequent intervals of the experiments. This was true for feeding larvae (Fig. 1A) and non-feeding prepupae (Fig. 1B) in experiments with either 5 or 15 *L. flavus* worker ants (Wilcoxon-test, $p < 0.02$ for all comparisons between first and second 3-minute experimental interval). On average, 1-2 droplets were delivered by feeding larvae, and 2-3 by non-feeding prepupae, in the initial three minutes. This compares to 1-2 droplets (feeding L4) or 3-5 droplets (prepupae) in the subsequent 12 min.

Virtually the same pattern occurred with the TO eversions. Feeding larvae everted their TOs significantly more often in the first 3 min than later (Wilcoxon-test, $p < 0.01$ for experiments with both 5 and 15 ants), and in the final 9 experimental minutes TO eversions were very rare (Fig. 2A). The same was observed with non-feeding prepupae (Wilcoxon-Test, $p < 0.01$), but the effect was delayed in the experiments with 15 ants to the third 3-min interval (Fig. 2B). Overall, TO eversions occurred more frequently in the prepupae during the final 9 experimental minutes.

The attractiveness of larvae to ants remained stable throughout the course of the experiments. All larvae were almost constantly tended from their first encounter with ants. Total tending times were 12:45-15:00 min in experiments with five *L. flavus* ants (only five feeding L4 and four prepupae had association times shorter than 15:00 min), and 13:27-15:00 min in trials with 15 ants (three prepupae had association times lower than 15:00 min). Within 1-2 min after the first encounter, the number of tending ants in all experiments reached the average level. Rarely there was a further slight increase, but never a distinct drop, in the number of tending ants with time.

## Comparison between feeding mature larvae and non-feeding prepupae

There was a distinct difference in DNO secretion rates between feeding larvae and prepupae (Fig. 3). During both experimental series with either 5 or 15 ants, prepupae produced much more secretion droplets than feeding fourth instars (U-test, $p < 0.002$, with or without the first 3 min of each experiment being included).

Due to the numerical preponderance of TO eversions in the initial 3 min of each experiment, the total frequency of TO eversions throughout the 15-min trials showed no significant differences between the two larval age classes ($p > 0.20$ for eversion rates in 15 min, with both 5 and 15 ants). When the initial 3 min were deducted, a significant difference emerged in the 15-ants series: prepupal larvae everted their TOs significantly more often than feeding fourth instars (U-test, $U_{19,20} = 114$, $p < 0.05$). In the 5-ants series, a similar, albeit non-significant difference between the two age classes occurred.

In experiments with 5 ants, the actual tending level (mean number of tending ants per larva) increased slightly, but significantly, from the
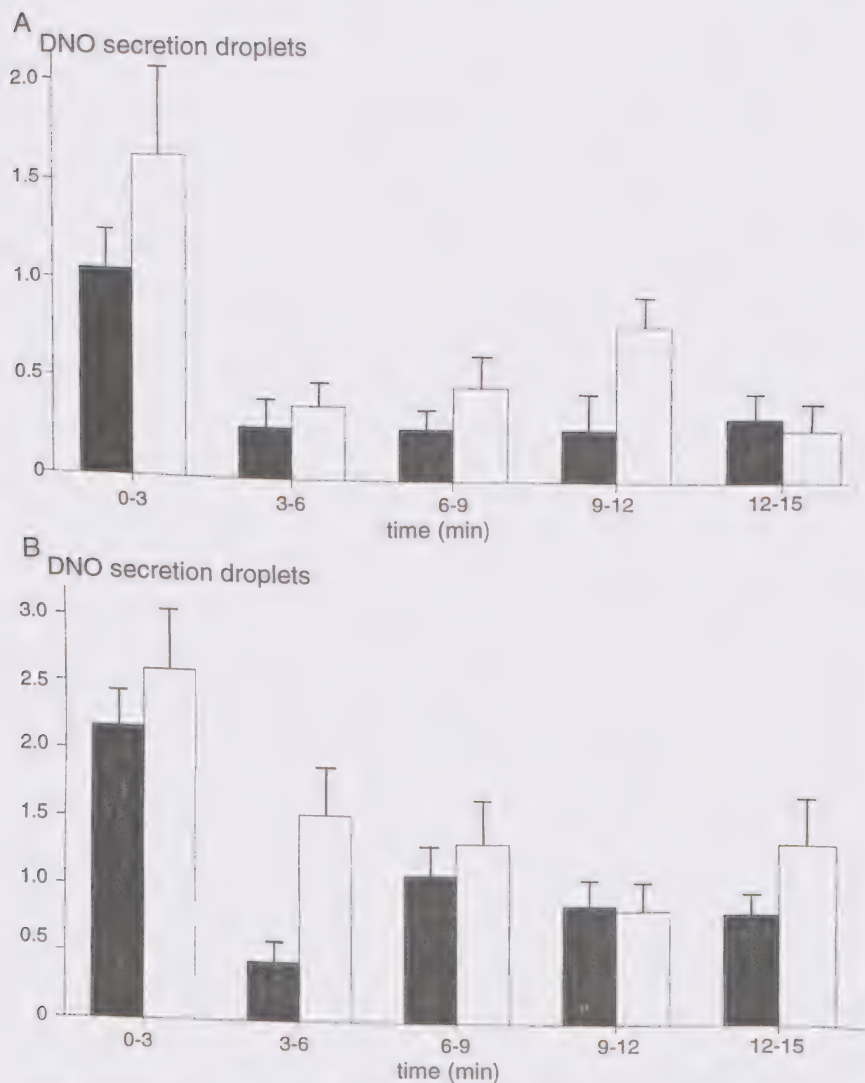
Fig. 1: Temporal pattern of DNO secretion acts observed in experiments with larvae of *Zizeeria knysna*. Given are means + standard errors for five successive 3-min time intervals. Hatched bars: with 5 *Lasius flavus* ants; white bars: with 15 ants. A): feeding mature fourth instars (n = 19 with 5 ants; n = 20 with 15 ants); B): non-feeding prepupae (n = 18 with 5 ants; n = 20 with 15 ants). Initial secretion rates are significantly higher than in subsequent 3-min intervals intervals (Wilcoxon-test, p < 0.05).
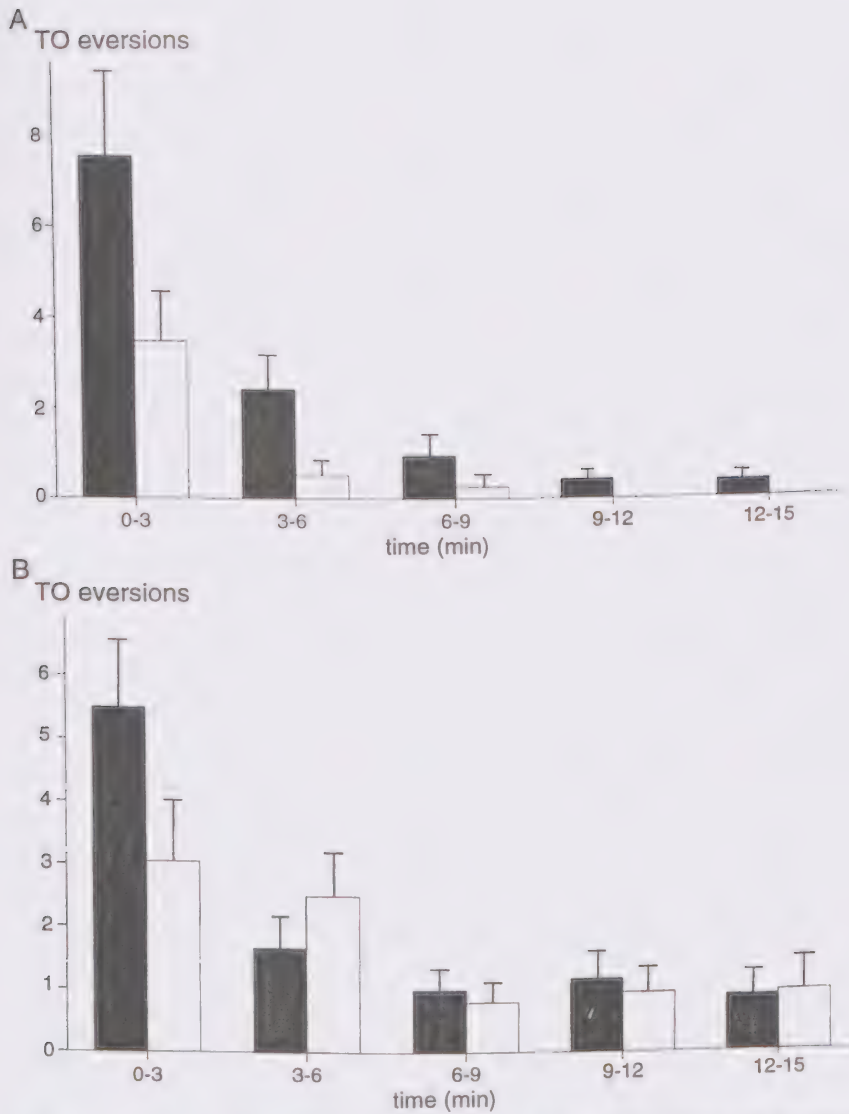
Fig. 2: Time course of TO eversion rates (means + S.E.) in *Z. knysna* larvae. Hatched bars: with 5 *L. flavus* ants; white bars: with 15 ants. A): feeding mature fourth instars (n = 19 with 5 ants; n = 20 with 15 ants); B): non-feeding prepupae (n = 18 with 5 ants; n = 20 with 15 ants). Initial eversion rates are significantly higher than in subsequent 3-min intervals (Wilcoxon-test).
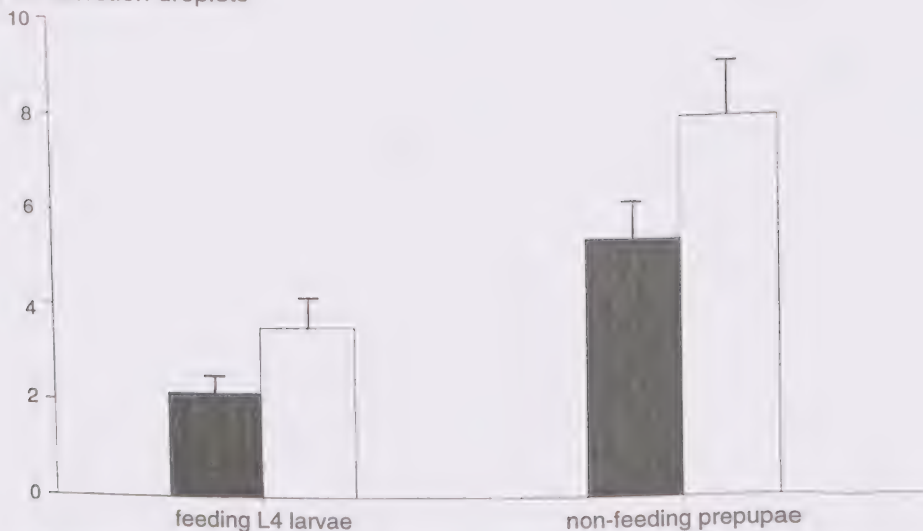
DNO secretion droplets



Fig. 3: Total number of DNO secretion droplets (means + S.E.) delivered in 15-min experimental intervals by larvae of *Z. knysna*. Hatched bars: with 5 *L. flavus* ants (n = 19); white bars: with 15 ants (n = 20). Differences between feeding larvae and non-feeding pupae, as well as between 5-ants and 15-ants trials are all statistically significant (U-test, p < 0.05).

feeding (2.63 ants/larva) to the non-feeding prepupal phase (3.13 ants / larva; $U_{18;19}$ = 100, p < 0.05). In the parallel series with 15 ants, larvae received an actual tending level of 5.35 ants/larva already during the feeding phase and this did not change with the transition into the prepupal stage (5.27 ants/larva). Hence, prepupal larvae attract a larger group of worker ants than still feeding mature larvae; however, under our experimental conditions an upper physiological limit ("saturation") is reached at an average of roughly 5 ants per larva.

**The influence of ant number**
   DNO secretions occurred more frequently among experiments with 15 ants, but this difference was only marginally significant for feeding larvae ($U_{19;19}$ = 133; p (1-tailed) < 0.10) or non-feeding prepupae ($U_{18;19}$ = 127; p (1-tailed) < 0.10) (Fig. 3). The same statistical trend was observed when the secretion events of the initial 3-min intervals were removed.
   No consistent result was obtained with respect to TO eversions. Feeding larvae everted their TOs more frequently in experiments with fewer ants present (p < 0.02), but this difference largely disappeared in the prepupal stage (p > 0.20).
   The actual mean tending level increased from 2.63-3.13 ants/larva in

the 5-ant trials to 5.27-5.35 ants/larva in the 15-ant experiments. A threefold increase in the number of available mutualists thus resulted only in an increase of the tending level by a factor of 1.7-2.0. In the 5-ant series, larvae or prepupae attracted on average 52-62% of their available mutualists, whereas in the 15-ant trials only 35% of the ants actually tended the lycaenid immatures. Maximum tending levels were, however, much higher. Two prepupal larvae attracted 8.29 and 9.63 ants, respectively (averaged over the 15 min period). These two animals were tended by 10-11 ants over several minutes and were then literally covered.

## Rank correlations

Neither at the feeding stage nor in the prepupal phase was the DNO secretion rate significantly correlated with body mass ($r_s$ values ranged from -0.006 to 0.318, $p > 0.10$). We also failed to detect significant correlations between the frequency of TO eversions and DNO secretion rates ($r_s$ ranging from -0.244 to 0.017, $p > 0.17$), or between TO eversion rates and actual tending levels ($r_s$ between -0.304 and 0.154, $p > 0.12$). Correlations did, however, occur between actual tending level and DNO secretion rates (feeding larvae: $r_s = 0.336$, $p = 0.093$ (with 5 ants); $r_s = 0.381$; $p = 0.066$ (with 15 ants); prepupae (with 15 ants): $r_s = 0.535$, $p < 0.01$). Similar correlations were obtained, when the DNO secretion data from the initial 3 min of each trial were removed.

These results suggest that DNO secretion and TO eversion rates are independent from one another and that body mass plays at most a minor role in the myrmecophily of *Z. knysna* immatures. A larger ant guard is somewhat more effective in stimulating more frequent DNO secretions, but this relationship is far from being close.

## Estimates of individual lifetime production of DNO secretions

Based on our experimentally established figures for average DNO secretion rates of *Zizeeria knysna* larvae, we here develop a model to estimate the total lifetime investment of individual larvae in these secretions. For this purpose, we assume that a) our experimental values of secretion rates are representative, and b) secretion rates remain largely constant once a larva-ant association is established. Therefore, we only use the average secretion rates from the final 12 min of our experiments because at the beginning of larva-ant interactions secretions occur more frequently for a short period of time (see above). Accepting these premises, hourly DNO secretion rates are as follows:

- with 5 ants per trial (i.e. actual tending level 2.63-3.13 ants/larva): feeding L4 1.1 droplets/12 min = 5.5 droplets/h; prepupae 3.3 droplets/12 min = 16.5 droplets/h;
- with 15 ants (i.e. actual tending level 5.3 ants/larva): feeding L4 1.9 droplets/12 min = 9.5 droplets/h; prepupae 5.1 droplets/12 min = 25.5 droplets/h.

In our laboratory culture the active feeding period of fourth instars

lasted 4 days and the larvae remained about one day in the non-feeding prepupal phase. Clark & Dickson (1971) recorded a developmental time of 6-7 days for the entire fourth instar in South Africa, hence our laboratory animals grew somewhat faster than under subtropical field conditions.

Furthermore, we assume that a *Z. knysna* larva is tended by ants for at least 8 h daily throughout the fourth instar. For comparison, we also calculate secretion rates under the assumption of a permanent (24 h daily) ant-association. We assume that the period of increased secretion rates within the prepupal phase does not exceed 8 h because the non-feeding prepupa then becomes fully immobile and the DNO non-functional. Field data on tending levels of *Z. knysna* are not yet available, but observations on many other facultatively myrmecophilous lycaenids suggest that it is realistic to postulate 8-24 h daily tending by 2-5 ants per larva. Our model hence provides upper and lower limits for lifetime DNO secretion amounts.

Under these assumptions, a *Z. knysna* L4 in our 5-ant trials would secrete 308 (8-hour ant association) to 660 (permanently ant-tended) droplets from its DNO. The respective values for the 15-ant trials are 508 (8 h) to 1116 droplets (24 h).

The diameter of secretion droplets was determined using a calibrated eye-piece on the stereomicroscope. DNO droplets of *Z. knysna* larvae measured $0.233 \pm 0.061$ mm in diameter (n = 6, range 0.15-0.30 mm), corresponding to a mean droplet volume of 0.00662 µl. For the following calculations, we used an average droplet diameter of 0.2 mm (volume 0.00419 µl) to avoid overestimation. The lifetime secretion volumes of individual *Z. knysna* larvae can thus be estimated to range from 1.3-2.8 µl in 5-ant trials and from 2.1-4.7 µl in 15-ant trials.

Data on the energy content of DNO secretions are unavailable for *Z. knysna* or any closely related lycaenid butterflies. In the facultatively myrmecophilous European species *Polyommatus (Lysandra) hispanus* (Herrich-Schäffer, 1852) and *P. icarus*, the secretions contain approximately 15 % carbohydrates (Maschwitz et al. 1975). If we assume a similar composition of DNO secretions for *Z. knysna*, then the individual lifetime secretion volumes are equivalent to 0.2-0.42 mg (5 ants) or 0.32-0.71 mg carbohydrates (15 ants).

The mean dry weight $\pm$ SD of adult specimens (males and females pooled) from our laboratory culture was $2.78 \pm 0.71$ mg (range 1.2-4.5 mg, n = 43). In relation to the average adult weight, the estimated carbohydrate content of larval DNO secretions is equivalent to 7.2-15.1 % (5-ant trials) or 11.5-25.5 % (15-ant trials).

## DISCUSSION

### Temporal patterns of interactions

Interactions between *Zizeeria knysna* larvae and ants show a clear

temporal pattern: DNO secretions as well as TO eversions occur most
frequently at the very beginning of a myrmecophilous association and
rapidly decrease to a rather constant and much lower level. This general
pattern occurred in both age classes and with both ant densities tested.
Similar results have been obtained with additional Palearctic lycaenid
species *(Polyommatus candalus* (Herrich-Schäffer, [1851]): Fiedler et al.
1994; *Polyommatus icarus*: Burghardt 1994; *Aricia agestis* ([Denis &
Schiffermüller], 1775): Hummel 1994; *Polyommatus daphnis* ([Denis &
Schiffermüller], 1775), *P. coridon* (Poda, 1761), *Glaucopsyche alexis*
(Poda, 1761): Fiedler, unpubl.). The phenomenon, however, is not univer-
sal. In larvae of *Celastrina argiolus* (Linnaeus, 1758) tested in exactly the
same manner, the clumped occurrence of DNO secretions and TO
eversions at the beginning of experimental interactions was not appar-
ent (Burghardt 1994).

Three mechanisms could be responsible for this effect: a fixed "physi-
ological" reaction to empty a full DNO reservoir; a response to distur-
bance and handling; or an increased initial investment to intensify ant-
associations from the very beginning of an interaction. All experimental
larvae had not been "milked" by ants for one or more days (and some
never before in their life) and hence probably had well filled secretion
reservoirs. One might assume that larvae at first deliver, in a kind of
"fixed action pattern", the entire reservoir content at a relatively high
rate, whereas later secretion acts can only be continued at a rate equal
to the physiological capacity of secretion supply replacement. Then, the
high initial secretion rate would be a non-adaptive epiphenomenon.

However, most *Z. knysna* larvae secreted only 1-3 DNO droplets in the
initial 3 min, which is most probably less than their reservoirs' capacity.
In *Polyommatus icarus* and *Aricia agestis* we estimated the DNO reser-
voir volume of larvae using Malicky's (1969) histological data on the size
of DNO gland cells (Fiedler, Burghardt & Hummel, unpubl.). According
to these data, a well-filled DNO reservoir should contain 10 droplets or
more. Furthermore, high initial rates of TO eversions accompanied the
enhanced DNO secretion rates. It is therefore unlikely that *Z. knysna*
larvae in our experimental setup really delivered all their stored secre-
tion resources, when interactions with ants commenced.

Alternatively, the larvae may have responded to the inevitable distur-
bance and handling when introduced into the experimental arena.
Leimar and Axén (1993) have shown that lycaenid larvae may respond
to tactile disturbance with a temporary increase in DNO and TO activity.
According to their data, and our own experiments with *Polyommatus
icarus* and *P. coridon* (Fiedler, unpubl.), the effect of mild tactile distur-
bance is in the range of one additional secretion droplet. This is exactly
the increase we found at the beginning of experiments with *Z. knysna*,
while in *P. icarus* and *Aricia agestis* the difference between initial
secretion rates per 3-min interval and subsequent 3-min intervals was

more distinct (2-4 additional droplets per 3 min: Burghardt 1994, Hummel 1994).

We suggest that the high initial secretion rate, accompanied by high TO activity, is an evolved adaptive behavior, although response to tactile disturbance may well be involved as a proximate factor. The very beginning of a larva-ant interaction is decisive for the subsequent stability of such an association. If a larva immediately provides an attractive food resource, it will be tended more constantly and may also induce the scout ant to recruit additional nestmates. The secretory behavior of *Z. knysna* larvae matches the "enticement and binding" strategy described by DeVries (1988). Increased initial activity of the TOs most likely serves the same function. Although previously debated controversially (Malicky 1969), TO eversions alert and activate tending ants, and their role in stabilizing larva-ant associations has been demonstrated at least in certain cases (Fiedler & Maschwitz 1988b, Ballmer & Pratt 1991).

Hence, temporal patterns of myrmecophilous interactions in *Z. knysna* larvae indicate what has been termed "strategic behavior" by Leimar & Axén (1993): caterpillars initially make a considerable effort (up to 9 droplets per 3 min) to establish an ant-association, but subsequently reduce this energetic investment to minimize costs. This finding has an important consequence. When lycaenid-ant interactions are studied in laboratory assays, the initial DNO secretion or TO eversion rates may be misleading. Observations should last until more or less stable "steady-state" conditions are reached. Experiments of short duration (e.g. 5-min trials by Ballmer & Pratt 1991) therefore become difficult to evaluate with respect to their ecological relevance.

## Increased myrmecophily in prepupae: adaptive trait or physiological epiphenomenon?

The investment of *Z. knysna* larvae in myrmecophily does not increase steadily with larval growth. In a couple of experiments with half-grown fourth instars of *Z. knysna* (6 with 5 ants, 3 with 15 ants; data not shown), DNO secretion and TO eversion rates were identical to the figures obtained with mature feeding L4 larvae. Furthermore, there was no positive significant correlation between larval weight and DNO secretion rates. Leimar & Axén (1993) and Burghardt (1994) likewise found that secretion rates were not correlated with either larval weight or age in feeding *P. icarus* larvae. Surprisingly, however, there is a rapid increase in secretion rates of *Z. knysna* immatures with the transition from the feeding to the non-feeding prepupal phase. Parallel effects have been observed in other Polyommatini species (*Polyommatus icarus*, *P. candalus*, *P. coridon*, *Aricia agestis*: Burghardt 1994; Hummel 1994; Fiedler et al. 1994 & unpubl.). The results of Wagner (1993) also indicate a particularly high investment into myrmecophily by prepupal *Hemiargus isola*.

Two possible mechanisms can explain this increase in prepupal secre-

tion rates. Perhaps larvae simply empty their DNO reservoirs because the secretions would be lost during pupation. Accordingly, one would expect all *Z. knysna* larvae to spontaneously give up their secretion reserves even if no ants are present. In hundreds of *Z. knysna* larvae reared with or without ants present we never observed such behavior. Spontaneous delivery of DNO secretions would also be risky because the liquid provides an ideal substrate for fungal or bacterial infection. However, spontaneous emptying of DNO reservoirs in captive, non-tended caterpillars does occur in at least two Oriental hairstreak species (*Rapala pheretima* (Hewitson, [1863]) and *Drupadia theda* (Felder & Felder, 1862)) with a very close, obligatory relationship to specific host ants (Fiedler, unpubl.).

We favor an adaptive explanation of increased myrmecophily in prepupae. Immobile prepupae and freshly moulted soft pupae would be particularly susceptible to attacks from predators. Furthermore, many lycaenid larvae descend from their hostplants and pupate at the base of the foodplant, in the soil or in shelters nearby. The probability of encountering ants in these situations should be even greater than on the hostplant, especially in habitats with a diverse fauna of ground-foraging ants. Therefore, prepupal lycaenid larvae should benefit from increased investment into myrmecophily because appeasement of potentially dangerous ants as well as their protection by ants against enemies would be enhanced. Once a stable association is formed between a prepupal larva and ants, this association is likely to persist throughout the pupal stage, when myrmecophily is mediated by pore cupola organs and dendritic setae.

## The influence of ant number

*Z. knysna* larvae responded to a change in tending levels with different activity rates of their myrmecophilous organs. TO eversions occurred more frequently in situations with fewer ants present (at the beginning of trials, in 5-ant experiments with feeding larvae). This coincides with the often repeated observation from numerous lycaenid species that TOs are mainly used to attract and "call" ants in situations when the tending level is low. Leimar & Axén (1993) further demonstrated that *P. icarus* larvae evert their TOs significantly more often after tactile disturbance. These observations indicate that lycaenid larvae receive a permanent feedback of information about their actual tending level, probably with the help of their mechanoreceptive hairs (e.g. Tautz & Fiedler 1992). This enables larvae to adjust their behavior to changing needs.

Even more interesting is the difference in DNO secretion rates in response to the tending level, although this effect was statistically only marginally significant. Stimulation of larvae by a 1.7-2.0-fold greater number of tending ants resulted in an increase of secretion rates by a factor of 1.5-1.7. The significant positive correlations between tending level and secretion rate provide further evidence in this direction.

Therefore, a higher actual tending level apparently exerts a stronger pressure on larvae to deliver secretions. This observation has two consequences. First, it shows that the costs of mutualism with ants are conditional and may depend on the density of mutualistic partners. Second, estimates of the lifetime energetic investment of larvae may critically depend on the tending levels employed to study larva-ant interactions.

Effects of tending ant numbers on secretory behavior of lycaenid larvae have as yet rarely been studied. Leimar & Axén (1993) reported that two worker ants received more droplets than single ants tending *P. icarus* larvae, whereas a further increase in ant-number did not further stimulate DNO secretions. In large experimental series with *A. agestis*, Hummel (1994) obtained similar data. In contrast, larvae of *Z. knysna* continue to adjust their secretory behavior at higher tending levels (increasing from 2.6 to 5.3 ants/larva). This has important consequences for the energetic benefits that ants may derive from tending lycaenid immatures. As long as larvae proportionately increase their investment with increasing stimulation, every additional ant tending a given larva will receive some reward. When the larva arrives at its physiological upper limit, additional tending ants may be beneficial to the larva (they strengthen the ant guard), but only add to the ants' foraging costs. Therefore, a delicate balance can be expected in most lycaenid-ant interactions. The dynamics and plasticity of most of these interactions remain to be studied.

In the 15-ants trials, larvae were relatively less effective in attracting ants. There was no proportional increase in actual tending levels with a threefold increase in available mutualists. Thus, beyond a certain tending level, additional ants receive too little reward to stay with the larvae for longer periods. At such a level the larva-ant interaction is numerically saturated, although higher tending levels (up to 11 ants/larva) could occasionally be observed for short periods of time. It remains to be determined whether the saturation level (5-6 ants per larva) in our experiments with *Z. knysna* is equivalent to optimal tending levels under natural conditions. Furthermore, "optimal" levels may again be conditional, depending on the ant species involved, larval age, time of day, population density of mutualists or enemies, and other factors.

## Energetic investment in the mutualism

According to our estimates, individual *Z. knysna* larvae produce some 300-1100 DNO secretion droplets with a total volume of 1.3-4.7 µl, representing approximately 0.2-0.7 mg carbohydrates. How realistic are these estimates, and what do they tell about the cost-benefit relationships in the putative mutualism?

Our estimates are conservative in the following respects: 1) they are based on a short larval period (according to Clark & Dickson (1971) the fourth instar may take 1-2 days longer); 2) we discarded the contribution

of L2 and L3 larvae (at least L3 larvae have a functional DNO); 3) we ignored the secretions of pore cupola organs or other setal structures, which may contribute to an energy flow from larvae to ants (Pierce 1983); 4) we used a low droplet diameter, because in other species with larger data sets available 0.2 mm was the typical droplet size. We also did not include amino acids from the DNO secretions in our estimates, because only trace amounts of such chemicals have been found in two ecologically similar *Polyommatus* species (Maschwitz et al. 1975). In the Australian lycaenid butterflies *Jalmenus evagoras* (Donovan, 1805) and *Paralucia aurifera* (Blanchard, 1848) (both obligatory myrmecophiles in the tribe Theclini), amino acids play an important role in DNO secretions and average carbohydrate contents are much higher (34 % in *P. aurifera*, 10-55 % in *J. evagoras*) than the 15 % assumed here (Pierce 1983, Cushman et al. 1994).

On the other hand, laboratory experiments with the facultative myrme-cophile *Aricia agestis* revealed that DNO secretion rates further decrease with time in permanent, stable ant-associations (Hummel 1994). In this species, secretion rates determined in 30 min "short-term" trials overes-timate long-term "steady-state" secretion rates (determined after 24 h of continuous ant-attendance) by a factor of 2-2.5.

Using the secretion rates from our experiments, an increase in the duration of the fourth instar by 2 days adds only to a total secretion volume of 1.7-3.9 µl (5 ants) or 2.7-6.6 µl (15 ants). The third instar lasts 4 days (Clark & Dickson 1971, pers. observ.). If we assume that L3 secretion rates are comparable to those of feeding fourth instars, but secretion volumes account only for one fourth (average L3 larvae have roughly one fourth the body mass of half grown L4), then we arrive at 2.1-4.9 µl (5 ants) or 3.1-8.3 µl (15 ants), respectively. Compared to our original estimate (1.3-4.7 µl), this is a roughly two-fold increase. On the other hand, long-term secretion rates are probably overestimated by a factor of 2-2.5. Hence, these effects largely level out, and our estimates of investment in carbohydrate secretions appear to be reliable at least for the order of magnitude. We can not give, of course, any estimate of the energetic investment in pore cupola secretions or TO eversions, because the chemistry and energetics of these organs are still unknown.

In parallel experimental series with additional lycaenid species (*Polyommatus icarus, P. candalus, Aricia agestis, Celastrina argiolus*; all facultative myrmecophiles) we arrived at similar figures for lifetime investments (Burghardt 1994; Hummel 1994; Fiedler et al. 1994). In these latter species, estimates of individual lifetime secretion volumes ranged from 0.5-10 µl. This concordance strengthens our conclusion that lifetime secretion volumes of some 1-5 µl correctly denote the order of magnitude of energetic investment into the symbiosis with ants in *Z. knysna*.

In a previous pioneering study, Fiedler & Maschwitz (1988a) estimated individual lifetime secretion volumes in the strong, but facultatively myrmecophilous species *Polyommatus (Lysandra) coridon*, arriving at

figures of 22-44 µl. This estimate is about one order of magnitude higher than our recent data on a couple of additional facultative myrmecophiles. What are the reasons for this discrepancy? First, *P. coridon* larvae develop much more slowly (under Central European field conditions, the third plus fourth instar of this obligately univoltine species take more than 4 weeks). Hence, individual larvae are available as mutualists for longer periods and they are almost constantly milked by ants. Second, the high secretion rates at the beginning of larva-ant interactions were not specifically controlled for in the 1988 model. Enhanced secretion rates of prepupae were also unknown at that time, and the non-feeding prepupal phase is particularly long (2-4 days) in *P. coridon*. According to recent data (Fiedler, unpubl.), more realistic average secretion rates are 6.5-10.5 droplets/h (feeding L4) and 21.5-29.5 droplets/h (non-feeding prepupae), respectively. Introduced into the model estimate, the calculated lifetime secretion volumes are 5.8-8.7 µl (8 h ant-tending) or 17-26 µl (permanent ant-association). Hence, the 1988 model for *P. coridon* may overestimate the secretion amounts by a factor of 2-5, but the energetic investment in myrmecophily remains about 4-6 times as high in this latter species than, for example, in *Z. knysna*.

    *Z. knysna* larvae allocate an estimated dry weight of carbohydrates equivalent to 7.2-25.2 % (depending on the estimate model and tending level) of their final adult dry body mass into their DNO secretions. At first glance, this suggests myrmecophily is a costly life-history asset. However, this interpretation can be qualified by two arguments. First, if larvae largely secrete carbohydrates, they reward the ants with a class of energy-rich substances which larvae as well as adult butterflies can easily replace from their foliage or nectar food, respectively. Second, ant-tended larvae of various lycaenid species overcompensate for the costs of myrmecophily. Thus, *P. icarus* and *A. agestis* larvae tended by *Lasius flavus* or *L. niger* pupate at weights increased by 10-12 % compared with untended controls (Fiedler & Hölldobler 1992; Hummel 1994). In *Hemiargus isola*, the developmental weight benefit is about 7 % when tended by *Formica perpilosa* (Wagner 1993). Weakly beneficial effects or complete compensation were also observed in other European lycaenid species (Fiedler & Saam 1994), while in the Australian obligate myrmecophile *Paralucia aurifera* the developmental benefits to the larvae are extraordinary (Cushman et al. 1994). Obviously, many examples of facultative interactions between lycaenids and ants, and even some cases of obligate myrmecophily, are low-cost strategies from the larval point of view.

    Individual *Z. knysna* larvae deliver 0.2-0.7 mg carbohydrates (even the highest estimate for a seven-day L4 period, including four-day L3, totals only 1.25 mg), representing a physiological energy content of 3.4-12 J (max. 21 J). Worker ants typically have a carbohydrate-based metabolism (e.g. Duncan & Lighton 1994), but how much can ants benefit from

the small quantity of energy delivered by the larvae they tend? We here use three approaches to give a rough estimate of this benefit.

Nielsen (1972; see also Peakin & Josens 1978) estimated the energy required to maintain an average mature colony of *Lasius alienus* throughout an annual cycle. During the hottest month, July (average soil temperature 23 °C), a 14500 worker ant population required 4243 J per day (0.34 J/d per ant). The ca. 5 J energy content secreted by one *Z. knysna* immature is equal to 14.7 ant-days. In other words, based on the secretions of a single larva, three worker ants can be maintained for a period of 5 days (the same period that a *Z. knysna* larva needs to pass through its final instar).

Nielsen (1986) provided a general regression between energy consumption and size in ants. Using his data, an ant with a dry mass of 1 mg has an energetic requirement of 0.036 J/h at 25 °C (5 mg dry mass: 0.17 mg/h). Then 5 J suffice to nourish a 1-mg ant (dry weight) for 5-6 days (5-mg ant: 30 h). Characteristic tending ants of lycaenids in Mediterranean climates (e.g. *Pheidole, Crematogaster, Lasius, Tapinoma*) are well within this range of dry mass or are even smaller.

Finally, Duncan & Lighton (1994) measured energetic costs of locomotion in two desert honeypot ant species of the genus *Myrmecocystus*. Based on their data on *M. mexicanus* at 30 °C, 5 J carbohydrate energy would suffice to cover the standard metabolic rate of a worker ant (wet mass 13.4 mg) for 3-4 days. These three calculations demonstrate that, even based on our lowest estimate, DNO secretions of *Z. knysna* larvae are a small, but nevertheless valuable contribution to the nourishment of ant colonies. If higher secretion amounts should prove more realistic, or if the additive effects of a population of larvae co-occurring in the foraging area of an ant colony is considered, the ants' reward is higher. Furthermore, our estimate ignores secretions of alternative myrmecophily organs (pore cupolas, dendritic setae).

Why do ants not attack and consume larvae, if these produce rather little reward? First, the epidermal secretions of lycaenid immatures clearly manipulate the ants' behavior in a way that suppresses aggressiveness. Larvae are groomed as if they were ant brood. While the chemical nature of the involved "adoption" (Pierce 1983) or "appeasement" substances (Maschwitz et al. 1985) remains unclear, behavioral experiments as well as preliminary chemical bioassays convincingly demonstrate this substance. Second, if ants would attack and consume a young L3 larva (at the time when myrmecophily would start) instead of milking it throughout the larval period, their energetic reward would not be higher. A freshly moulted L3 caterpillar has a wet weight body mass of less than 3 mg, or ca. 0.45 mg dry weight. Apart from indigestible cuticle, this mass mainly consists of proteins representing a physiological energy equivalent of ca. 8 J. This approximates the lowest estimate of energetic benefits provided by larval secretions.

Hence, in energetic terms the larva-ant symbiosis seems balanced in

the case of *Z. knysna*. Tending ants, however, must pay additional fitness costs (mortality risk while tending or traveling between nest and larvae, energetic costs of locomotion). Therefore, the larvae appear to derive a greater benefit from ant-tending (immunity against ant attacks, potential protection against parasitoids and enhanced development) than the ants do from harvesting minute secretion amounts. Without the "manipulative" action of the epidermal "adoption substances" such larva-biased symbioses certainly would not persist.

In conclusion, our experimental study revealed that a) interactions between *Zizeeria knysna* larvae and *Lasius flavus* ants show a characteristic temporal pattern with high activity of the myrmecophilous organs at the beginning of an encounter; b) that prepupal larvae invest distinctly more energy in myrmecophily compared to feeding larvae; and c) that a higher tending level can induce more frequent secretion acts. In energetic terms, facultative myrmecophily of *Z. knysna* is a low-cost interaction, which offers relatively small nutritive benefits to the ants, but considerable benefits to the butterflies. These avoid ant-predation, and may possibly be protected against enemies (e.g. Pierce & Easteal 1986). Hence, the interaction, although still potentially mutualistic, bears traits of manipulation and "strategic" economic resource use besides cooperative behavior.

## LITERATURE CITED

BALLMER, G. R. & G. F. PRATT. 1991. Quantification of ant attendance (myrmecophily) of lycaenid larvae. J. Res. Lepid. 30:95-112.

BAYLIS, M. & N. E. PIERCE. 1991. The effect of host plant quality on the survival of larvae and oviposition by adults of an ant-tended lycaenid butterfly, *Jalmenus evagoras*. Ecol. Entomol. 16:1-9.

BURGHARDT, F. 1994. Untersuchungen zum Einfluß der Futterqualität auf die Myrmekophilie von Bläulingsraupen. [v] + 94 + 43 pp. Diplom thesis, Univ. Würzburg.

CLARK, G. C. & C. G. C. DICKSON. 1971. Life histories of the South African lycaenid butterflies. Purnell, Cape Town. xvi + 272 pp., 108 pls.

COTTRELL, C. B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zool J. Linn. Soc. 79:1-57.

CUSHMAN, J. H., V. K. RASHBROOK & A. J. BEATTIE. 1994. Assessing benefits to both participants in a lycaenid-ant association. Ecology 75:1031-1041.

DUNCAN, F. D. & J. R. B. LIGHTON. 1994. The burden within: the energy cost of load carriage in the honeypot ant, *Myrmecocystus*. Physiol. Zool. 67:190-203.

DeVries, P. J. 1988. The larval ant-organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. Zool. J. Linn. Soc. 94:379-393.

Fiedler, K. 1989. Differences in the behaviour of ants towards two larval instars of *Lycaena tityrus* (Lepidoptera: Lycaenidae). Dt. entomol. Z., N.F. 36:267-271.

——. 1990. Effects of larval diet on the myrmecophilous qualities of *Polyommatus icarus* caterpillars (Lepidoptera: Lycaenidae). Oecologia 83:284-287.

——. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner zool. Monogr. 31:1-210.

Fiedler, K. & B. Hölldobler. 1992. Ants and *Polyommatus icarus* immatures (Lycaenidae) - sex-related developmental benefits and costs of ant attendance. Oecologia 91:468-473.

Fiedler, K. & U. Maschwitz. 1988a. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). II. Lycaenid larvae as trophobiotic partners of ants - a quantitative approach. Oecologia 75:204-206.

——. 1988b. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). III. New aspects of the function of the retractile tentacular organs of lycaenid larvae. Zool. Beitr. Berlin, N.F. 31:409-416.

——. 1989. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). I. Release of food recruitment in ants by lycaenid larvae and pupae. Ethology 80:71-80.

Fiedler, K. & C. Saam. 1994. Does ant-attendance influence development in 5 European Lycaenidae butterfly species? Nota lepid. 17(1):5-24.

Fiedler, K., K. G. Schurian & M. Hahn. 1994. The life-history and myrmecophily of *Polyommatus candalus* (Herrich-Schäffer) from Turkey (Lep., Lycaenidae). Linn. Belg. 14(6):315-332.

Hummel, V. 1994. Untersuchungen zum Einfluß der Dauer einer Ameisenassoziation auf die Sekretabgabe und andere Myrmekophilieparameter der Raupen des Bläulings *Aricia agestis* (Lepidoptera: Lycaenidae). [iv] + 120 + 23 pp. Diplom thesis, Univ. Würzburg.

Kutter, H. 1977. Hymenoptera: Formicidae. Insecta Helv. 6:1-298.

Leimar, O, & A. H. Axén. 1993. Strategic behavior in an interspecific mutualism: interactions between lycaenid larvae and ants. Anim. Behav. 46:1177-1182.

Malicky, H. 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). Tijdschr. Entomol. 112:213-298.

Maschwitz, U., M. Schroth, H. Hänel & Y. P. Tho. 1985. Aspects of the larval biology of myrmecophilous lycaenids from West Malaysia. Nachr. entomol. Ver. Apollo Frankfurt, N.F. 6:181-200.

Maschwitz, U., M. Wüst & K. Schurian. 1975. Bläulingsraupen als Zuckerlieferanten für Ameisen. Oecologia 18:17-21.

Nielsen, M. G. 1972. An attempt to estimate energy flow through a population of workers of *Lasius alienus* (Först.) (Hymenoptera: Formicidae). Natura Jutlandica 16:97-107.

——. 1986. Respiratory rates of ants from different climatic areas. J. Insect Physiol. 32:125-131.

PEAKIN, G. J. & G. JOSENS. 1978. Respiration and energy flow. Pp. 111-164 in: Brian, M.V. (ed.): Production ecology of ants and termites. Cambridge Univ. Press.

PIERCE, N. E. 1983. The ecology and evolution of symbioses between lycaenid butterflies and ants. Ph.D. thesis, Harvard Univ., Cambridge, Massachusetts.

——. 1989. Butterfly-ant mutualisms. Pp. 299-324 in: P. J. Grubb & J. Whittaker (eds.): Towards a more exact ecology. Oxford: Blackwell Science Publishers.

PIERCE, N. E. & S. EASTEAL. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. J. Anim. Ecol. 55:451-462.

PONTIN, A. J. 1978. The numbers and distribution of subterranean aphids and their exploitation by the ant *Lasius flavus* (Fabr.). Ecol. Entomol. 3:203-207.

SACHS, L. 1992. Angewandte Statistik. 7th edition. Springer, Berlin/Heidelberg/New York.

SCHURIAN, K. G. 1989. Revision der *Lysandra*-Gruppe des Genus *Polyommatus* Latr. (Lepidoptera: Lycaenidae). Neue entomol. Nachr. 24:1-181.

——. 1994. Beobachtungen zur Biologie und Ökologie von *Zizeeria knysna* (Trimen 1862) (Lepidoptera: Lycaenidae). Nachr. entomol. Ver. Apollo, Frankfurt, N.F. 15(1/2):47-56.

TAUTZ, J. & K. FIEDLER. 1992. Mechanoreceptive properties of caterpillar hairs involved in mediation of butterfly-ant symbioses. Naturwissenschaften 79:561-563.

WAGNER, D. 1993. Species-specific effects of tending ants on the development of lycaenid butterfly larvae. Oecologia 96:276-281.

WARNECKE, G. 1932/33. Übersicht über die bisher als myrmekophil bekannt gewordenen paläarktischen Schmetterlingsraupen der Familie Lycaenidae. Int. entomol. Z. Guben 26:165-171, 215-219, 238-242, 285-291, 375-378, 431-433, 460-462, 479-480, 514-516; 27:44-46, 121-127, 145-150, 178-180, 305-309, 3 pls.

# Survey of Adult Morphology in Nystaleinae and Related Neotropical Subfamilies (Noctuoidea: Notodontidae)

S. J. Weller

Dept. of Entomology, Univ. of Minnesota, St. Paul, MN 55108

**Abstract.** Based on a comparative study of 71 neotropical and 10 palearctic genera, morphological trends in Nystaleinae were ascertained. Over half the nystaleine species were examined (135 of 253). A diverse sample of neotropical Heterocampinae (27 of 37 neotropical genera, 46 species) and Hemiceratini (7 of 11 genera, 15 species) was also surveyed. Additional palearctic and nearctic notodontid species were examined in the more general study.

Survey results are presented along with illustrations of cephalic, thoracic and abdominal structures. Previous interpretations of internal tympanal structures are discussed, and sexually dimorphic structures described and illustrated. A checklist of nystaleine genera is provided. New morphological terms are proposed and synonyms are noted.

## INTRODUCTION

The family Notodontidae (Lepidoptera: Noctuoidea) consists of approximately 3,200 species worldwide (Holloway, Bradley, and Carter, 1987). The greatest diversity, over 1300 species, occurs in the New World tropics. Adults are usually heavy-bodied moths with pilose vestiture and cryptic coloration. Wingspans range from 127 mm (*Anurocampa mingens* Herrich-Schäffer, female) to as small as 20 mm (*Talmeca curtoides* Dognin, female). Notodontid larvae are notable for their often bizarre morphology, and some possess unique chemical defenses (cyanic acid, formic acid, and other ketones: Blum, 1981). Many species undergo striking ontogenetic changes between larval stadia, particularly in the Heterocampinae (Packard, 1895; Godfrey and Appleby, 1987). Notodontid larval host plants include both monocots and dicots (the majority on woody dicots), and larvae are usually either monophagous or oligophagous (Miller, 1992).

Little descriptive morphology is available for neotropical Notodontidae. Notodontid morphology is either discussed very generally based on few examples at the family or superfamily level (e.g., Brock, 1971; Richards, 1932), or discussed for only a few species within a faunal treatment or generic revision (e.g., Forbes, 1939a, 1948; Franclemont, 1948; Thiaucourt, 1975, 1980, 1985, 1987). Only recently has a comparative study among subfamily representatives been published (Miller, 1991).

In this paper, I describe and illustrate cephalic, thoracic and abdominal structures found in many notodontids, concentrating on Nystaleinae

(Tables 1, 2). The checklist of nystaleine genera (Table 1) is assembled from Weller (1989). Many of the following descriptions are new, because previous workers have concentrated on nearctic taxa. Most of my findings concern Nystaleinae, but I also comment on other taxa that illustrate character novelties or important character distributions. Previous interpretations of tympanal structures are discussed, and putative, pheromone-producing structures in males and females are described and illustrated. A summary of morphological terms and proposed equivalents is included.

## MATERIALS AND METHODS
### Preparation of specimens

Body parts (abdomens, appendages) or entire specimens (except wings) were softened in hot 10% KOH, then cleaned in several rinses of 40% ethanol. Genitalia were stained with either chlorozol black (dissolved in 20% ethanol), or with chlorozol black followed by saffranin (dissolved in 95% ethanol). Stained preparations were positioned, dehydrated, and mounted in either balsam or euparol. The membranous pleats of male genitalia trap water. Best dehydration results were obtained when positioned genitalia were left in sealed dissecting dishes of 95% ethanol for 4-12 hours. Antennae, labial palpi and legs were treated similarly, except that they were not stained. Wings were bleached, stained with Eosin Y, and mounted in balsam.

Softened whole-body preparations were prepared by first removing the abdomen. Either the head and prothorax were removed as a unit, or just the metathorax was removed. Once the viscera and scales were removed, preparations were stained with chlorozol black to enhance membrane contrast with the cuticle.

To examine the recessed tympanal membrane, I rotated the body wall so that the venter was 10 to 30 degrees above horizontal. Different preparations were used to expose the tympanum. In some, the isolated metathorax was entire. In others, midline dorsal and lateral cuts were made. The most satisfactory tympanal preparations resulted when the first abdominal tergum was left connected to the metathorax. In Table 3, the number of preparations is summarized. A complete list of species, sex, dissection numbers and type of dissection (e.g., whole body, genitalia) is available in Weller (1989).

### Sources of specimens

Material from the following collections was examined. Abbreviations follow Heppner and Lamas (1982): AMNH, American Museum of Natural History, New York (F.H. Rindge); BMNH, British Museum (Natural History), London (A. Watson); CAS, California Academy of Sciences, San Francisco (P.H. Arnaud); CMNH, Carnegie Museum of Natural History, Pittsburgh (J.E. Rawlins); CNC, Canadian National Collection, Ottawa, Canada (J.D. Lafontaine); CU, Cornell University, Ithaca, New York (J.K. Liebherr); DJ, D. Janzen, private collection, Univ. of Pennsylvania; LACM, Los Angeles County Museum, California (J.P. Donahue); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (J. Carpenter); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (R. Poole, R.K. Robbins); SJW, S.J. Weller preparation, University of Minnesota Insect Collection; UMO,

Table 1. Checklist of nystaleine genera examined (modified from Weller, 1989). Descriptions of new genera, and justifications of other taxonomic changes are given in Weller (1989, in prep.). Type species of new genera are provided below.

NYSTALEINAE: NYSTALEINI
Ankale Weller, NEW GENUS
        Lepasta, of authors [not Möschler, 1878]
                grammodes Felder, 1874 [Nystalea] NEW COMBINATION
                        conspicua Butler, 1878a [Lepasta] NEW SYNONYMY
Antiopha Schaus, 1901
        Tachuda Schaus, 1901, NEW SYNONYMY
        Naduna Schaus, 1901, NEW SYNONYMY
Bardaxima Walker, 1858b
        Gisara Schaus, 1901  NEW SYNONYMY
        Gozarta Walker, 1869
Calledema Butler, 1875
        Pseudantiora Kirby, 1892  REVISED STATUS
        Dasippia Draudt, 1932  NEW SYNONYMY
        Hippia, of authors [not Möschler, 1878]
Elasmia Möschler, 1886 REVISED STATUS
        Edema, of authors [not Walker, 1855]
        Harma Walker, 1858a NEW SYNONYMY
        Hippia, of authors [not Möschler, 1878]
Elymiotis Walker, 1857b
        Bardaxima, of authors [not Walker, 1858b]
        Cicynna Walker, 1858a
        Edema, of authors [not Walker, 1855]
        Gisara, of authors [not Schaus, 1901]
        Nystalea, of authors [not Guenée, 1852]
        Symmerista, of authors [not Hübner, 1821]
Euxoga Möschler, 1878
        Ctianopha Schaus 1901, NEW SYNONYMY
        Lysana, of authors [not Möschler, 1883]
Gopha Walker, 1862
Kryptokalos Weller, NEW GENUS
        Heorta, of authors [not Walker, 1858c]
                cilla Dognin, 1908 [Hippia] NEW COMBINATION
                    mitis Schaus, 1911 [Heorta]
                    oculata Dognin, 1909 [Lysana]
Lepasta Möschler, 1878
        Antiopha, of authors [not Schaus, 1901]
        Nystalea, of authors [not Guenée, 1852]
Lyricinus Weller, NEW GENUS
        Etobesa, of authors [not Walker, 1865b]
        Proelymiotis, of authors [not Schaus, 1901]
                xylophasioides Butler, 1878 [Etobesa], NEW COMBINATION

Lysana Möschler, 1883
  Proelymiotis, of authors [not Schaus, 1901]
Marthula Walker, 1856
  Edema, of authors [not Walker, 1855]
  Hippia Möschler, 1878, NEW SYNONYMY
  Phastia, of authors [not Walker, 1862]
  Pseudodryas, of authors [not Möschler, 1878]
  Xanthia, of authors [not Guenée, 1852]
Notoplusia Schaus, 1901
  Chadisra, of authors [not Walker, 1862]
  Crinodes, of authors [not Herrich-Schäffer, 1855]
  Rincodes Schaus, 1901, NEW SYNONYMY
Nystalea Guenée, 1852
  Antiopha, of authors [not Schaus, 1901]
  Congruia Dyar, 1908
  Cyrrhesta Walker, 1857b
  Eunystalea Grote, 1895
  Heterocampa, of authors [not Doubleday, 1841]
  Proelymiotis Schaus, 1901
Phedosia Möschler, 1878
  Bardaxima, of authors [not Walker, 1858b]
Phyllopalpia Draudt, 1932
  Antiopha, of authors [not Schaus, 1901]
Poresta Schaus, 1901, REVISED STATUS
  Edema, of authors [not Walker, 1855]
  Proelymiotis, of authors [not Schaus, 1901]
  Nystalea, of authors [not Guenée, 1852]
  Strophocerus, of authors [not Möschler, 1883]
Strophocerus Möschler, 1883
  Antiopha, of authors [not Schaus, 1901]
  Nystalea, of authors [not Guenée, 1852]
  Poresta, of authors [not Schaus, 1901]

NYSTALEINAE [SENSU LATO]
Bahaia Dyar, 1924
  Betola of authors [not Schaus 1901]
Dasylophia Packard, 1864
  Drymonia, of authors [not Hübner, 1819]
  Edema, of authors [not Walker, 1855]
  Elymiotis, of authors [not Walker, 1857b]
  Heterocampa, of authors [not Doubleday, 1841]
  Oedemasia, of authors [not Packard, 1864]
  Phalaena, of authors [not Linnaeus, 1758]
  Proelymiotis of authors [not Schaus, 1901]
  Symmerista, of authors [not Hübner, 1821]

Didugua Druce, 1891
Euharpyia Schaus, 1901
Lusura Walker, 1855
          Tifama Walker, 1855
          Chaetognatha Felder, 1874
Notela Schaus, 1901
Pentobesa Schaus, 1901
          Edema of authors [not Walker, 1855]
          Betola Schaus, 1901
          Nycterotis, of authors [not Felder, 1874]
          Proelymiotis of authors [not Schaus, 1901]
          Symmerista of authors [not Hübner, 1821]
          Tifama of authors [not Walker, 1855]
Symmerista Hübner, 1821
          Edema Walker, 1855

Table 2. List of other notodontid genera and species examined. Classification follows Forbes (1935), Weller (1989), Miller (1991), and Miller and Otero (1994).

Subfamily:  Genus species

DIOPTINAE
Dioptini
          *Dioptis trailii* Butler
          *Phryganidia californica* Packard
Josiini
          *Erbessa unimacula* (Warren)
          *Josia* sp.
          *Scotura nervosa* Schaus

DUDUSINAE
          *Dudusa sommeri* (Hübner)
          *Crinodes bellatrix* Stoll
          *Crinodes* sp.

HEMICERATINI[1]
          *Antaea juturna* Cramer
          *Apela strigatula* Forbes
          *Apela* sp.
          *Hapigia curvilinea* Schaus
          *H. nodicornis* Guenée
          *Hemiceras* near *pallidula* Guenée
          *Hemiceras* sp.

## HETEROCAMPINAE
Heterocampini

       *Heterocampa astarte* Doubleday
       *H. astartoides* Benjamin
       *H. guttivitta* (Walker)

Stauropini

       *Stauropus fagi* (Linnaeus)

Tribal affiliation unknown

       *Chadisra bipars* Walker
       *Chadisra* sp.
       *Disphragis notabilis* (Schaus)
       *D. tharis* (Stoll)
       *Farigia* sp.
       *Heorta roseoalba* Walker
       *Litodonta hydromeli* Harvey
       *Malocampa bolivari* (Schaus)
       *Pamcoloma marita* Schaus
       *Rhuda dimidiata* (Herrich-Schäffer)
       *R. focula* (Cramer)
       *R. splendens* (Druce)
       *Rifargia lineata* (Druce)
       *Rifargia* near *mortis* Schaus
       *Rifargia* near *onerosa* Schaus
       *Talmeca perplexa* Schaus
       *Urgedra striata* Druce

## NOTODONTINAE
Dicranurini

       *Cerura vinula* (Linnaeus)

Notodontini

       *Pheosia gnoma* (Fabricius]
       *P. tremula* (Clerck)

## PHALERINAE

       *Datana ministra* (Drury)
       *Nadata gibbosa* (J.E. Smith)

## PYGAERINAE

       *Clostera curtula* (Linnaeus)

## THAUMETOPOEINAE

       *Gazalina* sp.
       *Thaumetopoeia processionea* (Linnaeus)

INCERTAE SEDIS

*Anurocampa mingens* Herrich-Schäffer
*Canodia difformis* Herrich-Schäffer
*Lirimiris lignitecta* Walker[1]
*Lirimiris* sp.[1]
*Lobeza Smithi* Druce
*Zelica myops* (Felder)
*Zelica zelica* (Stoll)
*Zelica* sp.

[1] Miller (1991) places Hemiceratini and *Lirimiris* as *incertae sedis*

---

Table 3. Summary of specimens dissected. Classification follows Miller (1991)(M = male, F = female, g = genitalic preparation, w = whole body preparation).

| Taxon | No. of Genera | | No. of Species | | No. of Preparations | | | |
|---|---|---|---|---|---|---|---|---|
| | Total | Examined | Total | Examined | M-g | F-g | M-w | F-w |
| Nystaleinae | 31(25)[1] | 31 | 253 | 170 | 309 | 147 | 34 | 9 |
| Heterocampinae | 37 | 30(3[2]) | 398[3] | 34(4[2]) | 50 | 34 | 12 | 3 |
| Hemiceratini | 11 | 7 | 287 | 9 | 10 | 5 | 4 | 2 |
| Dioptinae | 40 | 3 | 400 | 3 | 4 | 5 | 3 | 3 |
| Notodontinae | 9[3] | 1(2[2]) | 14[3] | 2(2[2]) | 6 | 6 | 1 | 0 |
| Dudusinae | 7+[4] | 2 | 93+[4] | 3 | 3 | 1 | 1 | 0 |
| Phalerinae | 6+[4] | 5 | 88+[4] | 5 | 6 | 5 | 1 | 1 |
| Pygaerinae | ?[4] | 1 | ?[4] | 1 | 6 | 4 | 4 | 0 |
| *Lirimiris* | 1 | 1 | 16 | 2 | 2 | 1 | 0 | 0 |
| Thaumetopoeinae | 23 | 2 | 100 | 3 | 5 | 3 | 1 | 1 |

[1] 25 genera after revision (Weller, 1989)
[2] Old World taxa
[3] New World taxa only
[4] Estimates tentative or unavailable (= ?) (Miller 1991)

University Museum, Oxford University, Oxford, England; VOB, V.O. Becker, private collection, Brasilia, Brazil; ZMHB, Zoologisches Museum an der Humboldt-Universität zu Berlin, DDR-Germany (H.J. Hannemann). Figures list the museum collection and source slides or whole body preparation numbers (e.g., AMNH genitalia preparation SJW219).

## Terminology

Terminology for genitalic structures follows Forbes (1948), Sibatani et al. (1954), Sibatani (1972), and Klots (1970), except where I propose new terms. Terminology for the tympanum follows Richards (1932), Forbes (1916), and Kiriakoff (1950a), with reinterpretations of some structures. A lexicon and definitions of terms applicable to notodontid morphology is provided.

## MORPHOLOGY AND DISCUSSION
### Head (Figures 1-3)

The notodontid vertex is usually tightly scaled. Ocelli are present in some species (Forbes, 1948), but can be absent (e.g., *Litodonta hydromeli*: Heterocampinae). Often, a broad band of demelanized cuticle connects the ocelli across the vertex. In most species, the ocelli are located dorsal to the antennal scape and bordering the compound eyes (Fig. 1). The compound eyes are well developed, and the ocular index (frons width/ eye height) (Davis, 1975) ranges from 0.25 (*L. hydromeli*) to 1.0 (*Gazalina* sp.: Thaumetopoeinae) (Table 4). That is, *L. hydromeli* has very large eyes, and *Gazalina* sp. has very small eyes. Presumably, the ocular index and similar measures (eye width/frons width; Ferguson, 1985) reflect degree of night vision acuity. I have not surveyed intraspecific or intrageneric variation. Ferguson (1985) found that eye size may vary seasonally and geographically in arctiids.

The ventral border of the compound eyes and ventrum of the occiput often have long scales and hairs that partially cover the lower eye portion.
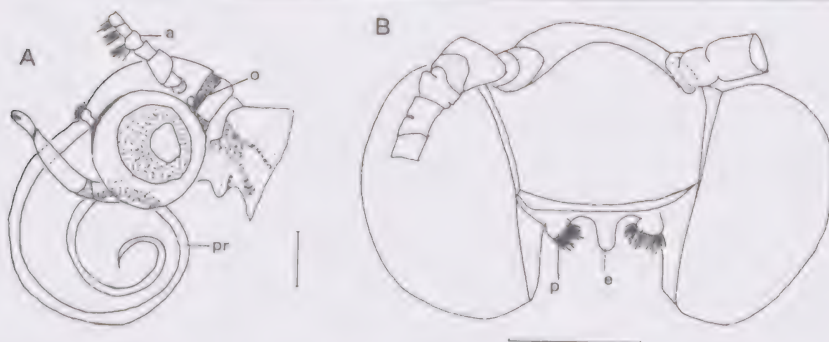


Figure 1. Descaled head of *Rifargia lineata* (NMNH 43,488, male). A. lateral view; B. frontal view. a = antenna, e = epipharynx, o = ocellus, p = pilifer, pr = proboscis. (Scale = 1.0 cm)

Table 4. Mouthpart structure development in the Notodontidae. a = absent, b = bumps, f = female, F/E = frons/eye ratio, ls = lacks setae, m = male, me = membranous, r = reduced, s = short, sc=sclerotized, se = setae present, prep# = dissection number, wd = well-developed, v = vestigial, vs = very short, + = present, - = absent.

| Genus species | Prep# | Frons width F(mm) | Eye diameter E(mm) | F/E | Pilifer | Condition of Proboscis | Maxillary palps No. of segments | Develop- ment |
|---|---|---|---|---|---|---|---|---|
| *Calledema* sp. | f346 | 1.0 | 1.92 | 0.52 | + | wd | 1 | me |
| *Cerura vinula* | m340 | 1.12 | 2.00 | 0.56 | ls | vs | a | - |
| *Chadisra bipars* | m437 | 0.72 | 1.72 | 0.42 | + | vs | 1 | me |
| *Crinodes* sp. | m449 | 1.68 | 3.24 | 0.52 | + | wd | 1 | me |
| *Dasylophia anguina* | m340 | 0.80 | 1.72 | 0.47 | + | s | 1 | me |
| *Dudusa sommeri* | m443 | 1.36 | 2.32 | 0.59 | + | wd | 2 | me |
| *Elasmia pronax* | m426 | 0.86 | 2.32 | 0.37 | + | wd | 2 | me |
| *Elymiotis ancora* | m347 | 1.56 | 2.36 | 0.66 | + | wd | 1 | me |
| *Farigia* sp. | m258 | 0.68 | 1.56 | 0.44 | + | v | 1 | me |
| *Gazalina* sp. | f445 | 1.36 | 1.36 | 1.00 | b | a | a | - |
| *Gopha mixtipennis* | f363 | 0.72 | 1.48 | 0.49 | + | wd | 1 | s |
| *G. mixtipennis* | m364 | 0.92 | 1.64 | 0.56 | + | wd | 1 | s |
| *Hapigia nodicornis* | m229 | 1.92 | 2.92 | 0.66 | + | wd | 1 | me |
| *Hemiceras* sp. | m262 | 1.36 | 1.76 | 0.77 | + | wd | 1 | me,r |
| *Josia* sp. | f259 | 0.78 | 0.98 | 0.80 | + | wd | 1 | ss |
| *Litodonta hydromeli* | m352 | 0.44 | 1.76 | 0.25 | vs | v | 1 | me,r |
| *Lysana plexa* | m364 | 1.32 | 2.08 | 0.63 | + | wd | 1 | s |
| *Nadata gibbosa* | m355 | 0.80 | 1.80 | 0.44 | + | v | 1 | me |
| *Notoplusia clara* | m349 | 0.96 | 1.80 | 0.53 | + | wd | 1 | me |
| *Nystalea* sp. | m263 | 1.24 | 2.80 | 0.57 | + | wd | 1 | me |
| *Pentobesa basitincta* | m395 | 0.92 | 1.76 | 0.42 | + | s | 1 | me |
| *Pentobesa xylinoides* | m341 | 1.2 | 2.12 | 0.57 | + | wd | 1 | me |
| *Rifargia* sp. | m261 | 1.44 | 2.20 | 0.65 | + | wd | 1 | me |
| *Stauropus fagi* | m438 | 1.0 | 1.68 | 0.60 | s | b | a | - |
| *Zelica zelica* | m451 | 0.72 | 1.48 | 0.49 | + | wd | 1 | me |
| *Zelica* sp. | m452 | 1.0 | 1.52 | 0.66 | + | wd | 1 | me |

Whether the head vesture is loose and "fuzzy" or tightly scaled varies between genera, but rarely within monophyletic genera.

Notodontid mouthparts can be absent, vestigial or weakly developed (Forbes, 1948; Bourgogne, 1951; Miller, 1991). For many holarctic species, cerurines and thaumetopoeines, vestigial or weak mouthparts are typical. However, the proboscis is well developed in most tropical notodontids including most Nystaleinae. Maxillary palpi are usually present, but in *Gazalina* are absent. They may be one- or two- segmented (Table 4) and either sclerotized or

membranous. The pilifer may be vestigial or well developed with stout setae (Fig. 1B). The size of the epipharynx varies, and its shape can be rectangular, bilobed, or round. When the proboscis is vestigial, associated structures are usually vestigial. Functional mouthparts indicate that adults probably feed and live a long time.

Labial palpi are usually three-segmented, and normally, the length of the third segment is approximately two-thirds the length of the second. However, the third segment can be much longer or much shorter (Fig. 2A-D), or the labial palpus can be reduced to two segments (Miller, 1991). As in most Lepidoptera, the organ of vom Rath is well developed. Typically, labial palpi are tightly scaled, although loose, long hairs can emanate from the first segment.

Notodontid antennae tend to be sexually dimorphic, with males possessing more complicated antennal structures (e.g., pectinations, cilia) than females (e.g., shorter cilia, scattered setae). Occasionally, antennae are monomorphic (*Gopha mixtipennis* Walker). Individual antennal segments can be cylindrical, bulbous or prismatic and an antenna may be composed of a combination of segment types. Segment shape and structure can vary between and within genera. Some examples of antennal variation are shown in Figure 3.

The antennal scape of most notodontids is rounded, although it can be elongate. In some species, compact clusters of scales arise from the scape. Forbes (1948) referred to these as antennal tufts. Antennal tufts may be either short and blunt-tipped (*Lirimiris* Walker), triangular (*Hemiceras* Guenée), or long, (e.g., *Nystalea, Phedosia, Pentobesa, Dasylophia*).

In males of *Hapigia* Guenée, the antennal scape and first segment are greatly modified. The first segment is greatly expanded and bowl-shaped. The pedicel is membranous dorsally and forms a hinge between the scape and first segment. The first segment locks into a groove on the scape, folding the distal part of the antenna over the back (Fig. 3F).

## Thorax (Figures 4-6)

The thorax is usually covered dorsally with moderately long scales and ventrally with long scales and hairs. The most obvious modifications occur on the prothorax and metathorax. Mesothoracic sclerites did not appear to vary among taxa.

**Prothorax**. The patagia are usually sclerotized and covered with scales. They are thought to be homologous with the membranous warts of Trichoptera (caddisflies) (Kristensen, 1984). Caudad to these, a second set of membranous or weakly sclerotized structures occurs in most species (Fig. 4a). These appear to be homologous with the noctuid parapatagia (Oseto and Helms, 1976). Development of parapatagia varies, and they are easily damaged when preparing a whole-body dissection. They are present in both sexes. Occasionally, a second, weakly developed, lateral pair of parapatagia occurs next to the spiracle (not illustrated, e.g. *Gazalina*). *Dudusa sommeri* (Dudusinae) appears to
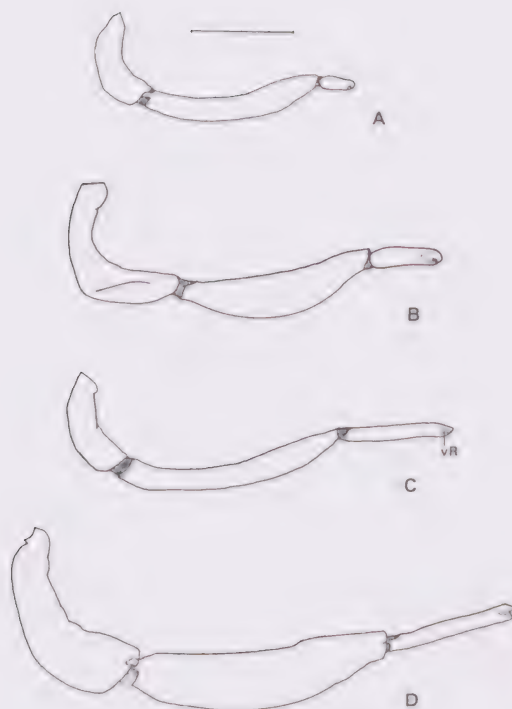
**Figure 2** Labial palpi (distal at right). A. *Notoplusia minuta*; B. *Nystalea virgula*; C. *Calledema jocasta*; D. *Nystalea corrusca*. vR = vom Rath's organ. (Scale = 1.0 mm)

possess a derived condition where parapatagia are absent and the patagia are enlarged and heavily sclerotized.

**Mesothorax and metathorax.** No variation was observed in most sclerites comprising these segments. The metathoracic furcae show some variation, and tympanal studies indicate that some thoracic novelties (e.g., double pocket IV, *Hemiceras* sp.) may be species-specific.

**Tympanum and associated structures** (Figs. 5, 6). As in other noctuoids, the notodontid tympanum occurs on the metepimeron. Notodontids are unique in that the tympanum is recessed; the tympanal membrane faces ventrally (Forbes, 1916; Richards, 1932; Sick, 1940; Kiriakoff, 1950a, 1950b, 1950c; Miller, 1991). The notodontid tympanal membrane lacks the nodular sclerite (Richards, 1932), and sclerotized abdominal hood associated with tympana in many Noctuidae, Arctiidae and Lymantriidae. In nearly all neotropical and some nearctic notodontids, the first abdominal spiracle occurs in a sclerotized, bowl-like depression which may act as a sound collector. In many holarctic species, the bowl is either weakly sclerotized or membranous. The genera *Hapigia* and
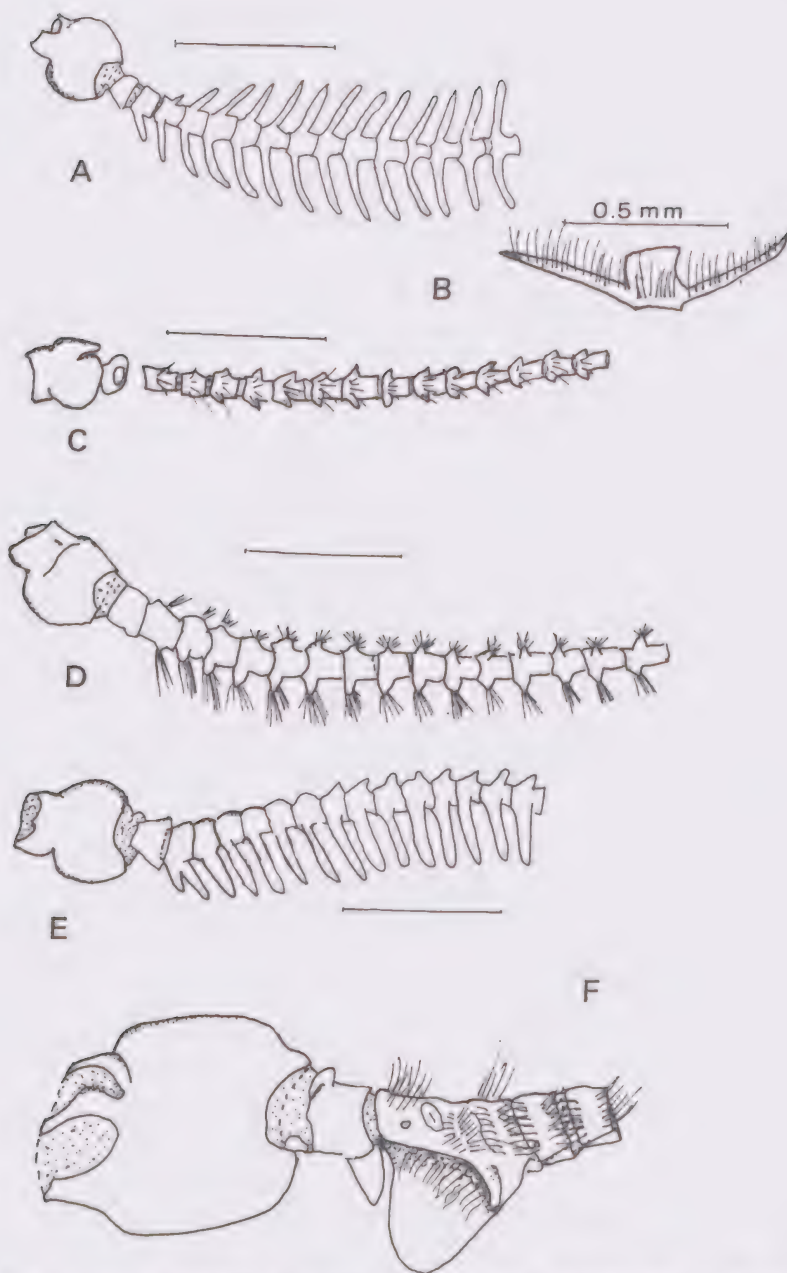
Figure 3 Antennal variation. A. *Notoplusia clara*, male, (bipectinnate); B. enlarged
    segment showing pectinations and cilia; C. *Notoplusia clara*, female
    (scattered setae); D. *Elymiotis ancora*, male (ciliate); E. *Canodia difformis*,
    male (unequally pectinnate); F. *Hapigia nodicornis*, male, showing basal
    enlargement. (Scale = 1.0 mm)
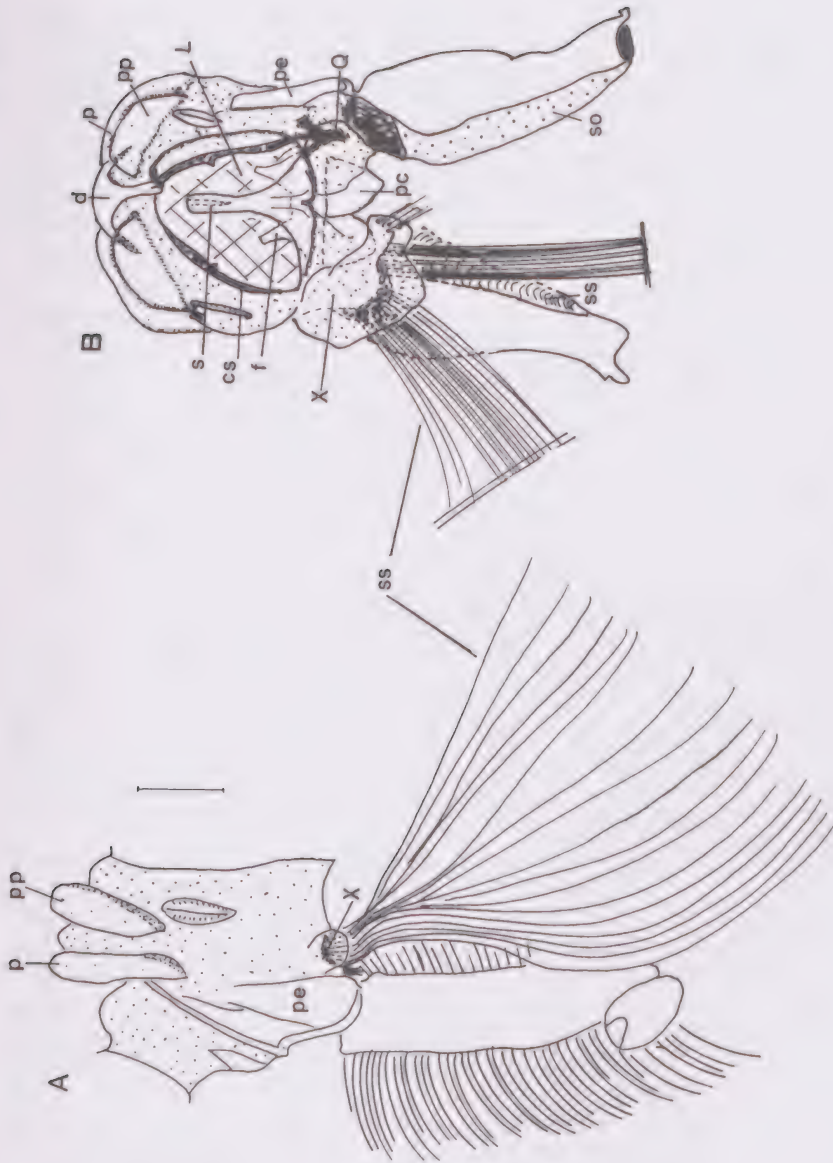
**Figure 4** Prothorax of *Hapigia curvilinea*. A. side view, anterior at left; B. posterior view with right scent brush flap removed. cs = cervical sclerite, d = dorsal plate of pronotum, f = furca, L = lumen, p = patagium, pc = precoxale, pp = parapatagium, pe= proepimeron, s = spina, Q = reinforced fusion point of furca, cervical sclerite, and proepimeron, X= modified membranous flap, so = putative scent organ, ss = scent scales. (Scale = 1.0 mm)

*Antaea* possess a large, membranous, pleural hood inflated with hemolymph that surrounds this sclerotized bowl. With isolated ear preparations, Fullard (1984) demonstrated that the pleural hood helps to localize sound waves, and that it increases the moth's ability to detect the direction of incoming signals.

The internal morphology of the notodontid tympanum has been described by Richards (1932) and Kiriakoff (1950a,b), but their interpretations conflict. Richards (1932) described tympana for the major noctuoid families, concentrating on Noctuidae. His terminology is generally applicable to notodontids.

For notodontids, Richards concluded that pockets I and II were small, pocket III was absent and pocket IV was present. He examined three nearctic species (*Datana angusi* Grote & Robbinson: Phalerinae, *Heterocampa guttivitta* Walker: Heterocampinae, *Clostera inclusa* Hübner: Pygaerinae) and two neotropical species (*Zelica zelica*: Pygaerinae, *Malocampa* near *sorex*: Heterocampinae). Re-examination of *H. guttivitta* shows that Richards misinterpreted the notodontid pockets. From his diagram (plate 10: Richards, 1932), it is apparent that he did not rotate the thorax sufficiently to view the pockets. Internally, notodontid tympana are very different from those of noctuids. The recessed tympanal membrane obscures the pockets, and pocket orientation is skewed. Using position and orientation of pocket openings as criteria of homology, I conclude that pockets I, III and IV are present in most notodontids, and that pocket II is often absent. Pocket II is sometimes difficult to see even when it is present. The notodontid structure that I interpret as pocket III, and that Richards termed pocket II, is positioned at the ventral rim of the tympanic membrane, with its opening into the body cavity facing dorsally (e.g., Fig. 5A).

Kiriakoff used tympanal studies to classify Notodontidae (e.g., Kiriakoff, 1950a, 1950b, 1950c), stressing different shapes of scutal phragma ("type notodontoid" vs. "type phalenoide") and tympanal structures, but Kiriakoff's tympanal interpretations were sometimes inconsistent. Distortion caused by preparing and viewing the thorax may explain discrepancies. For example, Kiriakoff described *Bardaxima marcida* Felder and *Gisara procne* Schaus as having differently shaped tympanal cavities (Kiriakoff, 1950c). *Gisara* is a junior synonym of *Bardaxima* (Weller 1989; Table 1), and the tympanal cavities of these two species are practically identical. Kiriakoff also disagreed with Richard's interpretation of tympanal structures and renamed pocket IV: "le support posterieur" (Kiriakoff, 1950a, 1950c). Notodontid pocket IV is usually open with its edges defined by an anterior and posterior internal ridge that extend from the tympanal cavity (timbal sensu Kiriakoff) to the furcal suture (Fig. 5: IVa, IVp). The anterior ridge (IVa) can be reduced or absent as in several notodontids that Kiriakoff examined (Kiriakoff 1950a, 1950c). In *Crinodes* Herrich-Schäffer, pocket IV is closed (Fig. 5E) like those of
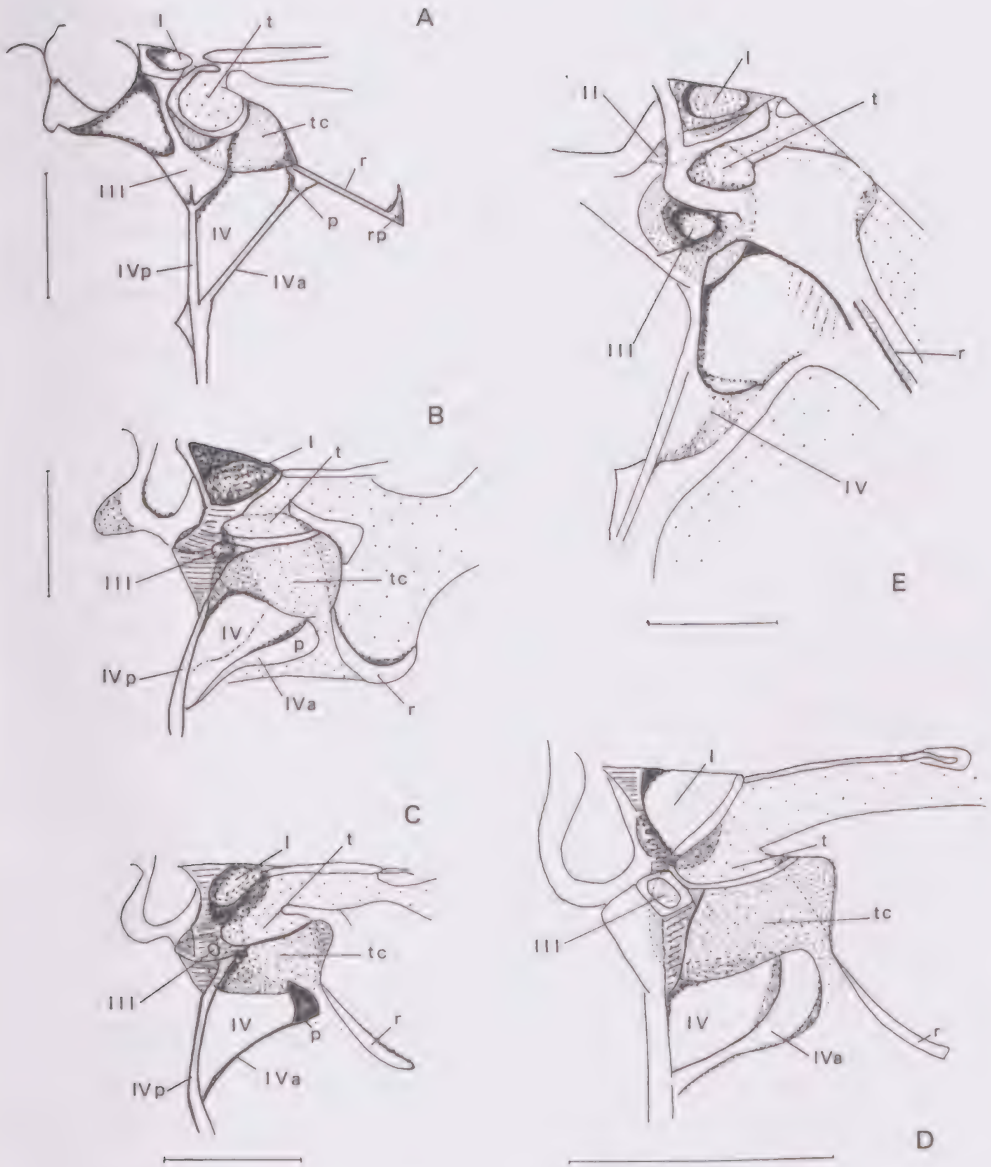
**Figure 5** Internal view of notodontid metathoracic tympana, anterior at right. A. *Rifargia lineata*; B. *Elymiotis ancora*; C. *Antiopha multilinea*; D. *Elasmia astuta*; E. *Crinodes* sp. I = pocket I, II = pocket II, III = pocket III, IV = closed pocket IV, IVa = anterior strut of open pocket IV, IVp = posterior strut of open pocket IV, p = anterior branch pocket of IV, r = pre-epimeral/epimeral ridge, rp = ridge pocket, t = tympanal membrane, tc = tympanal cavity. (Scale = 1.0 mm)

Noctuidae, supporting the homology of the posterior ridge of pocket IV and Kiriakoff's "support posterior."

A feature of pocket IV not mentioned by Kiriakoff is the tendency for a small pocket (p) to form on the dorsal end of the anterior support abutting the tympanal cavity (Fig. 5). This additional pocket can be elaborate as in some *Hemiceras*. Also, the degree of divergence between the anterior and posterior supports of pocket IV differs among species. They are normally at acute angles, but can also be at right angles to one another (e.g. *Pentobesa basitincta* Dognin).

In addition to pocket IV, the pre-epimeron/ epimeron boundary is often modified in notodontids. There may be a simple internal ridge or a pocketlike structure (Fig. 5A-E) that originates at the tympanal cavity and extends anteriorly. Kiriakoff termed this structure "support anterior de la timbale" (Fig. 5, r). This support occasionally fuses with the anterior edge of pocket IV as in *Anurocampa mingens* (Kiriakoff, 1950c: his fig. 11). This epimeral pocket and dorsal pocket of the anterior branch of pocket IV may provide additional resonating chambers.

Extensive tympanal variation occurs in the dioptines and thaumetopoeines (Richards, 1932; Sick, 1940). Many dioptines are brightly colored, mimetic and probably diurnal (Hering, 1925; Miller and Otero, 1994). The tympanum may be well developed, or reduced and rudimentary. In the five dioptine species examined, pocket II is absent in all, pocket III is absent in most, and pockets I and IV are absent when the tympanal cavity is rudimentary. In *Scotura nervosa*, *Josia* sp., and *Erbessa unimacula*, pockets I and IV are present and well developed, but pockets II and III are absent (Fig. 6A-C). These species also have a well-developed tympanal concavity that Richards referred to as a kettledrum structure (Richards, 1932: 38). This tympanal type is restricted to a subset of dioptine genera (Sick, 1940; Kiriakoff, 1950a; Miller and Otero, 1994). Miller and Otero (1994) use the presence of this kettledrum tymanal cavity to recognize the Josiini, formerly the Josiinae of Kiriakoff (1950a) and group V of Sick (1940).

The remaining dioptine genera are placed in the Dioptini (Miller and Otero, 1994), because they lack the kettle-drum type cavity. Reduced tympana in dioptines can occur in various ways. In *Dioptis trailii*, all pockets are absent, and the tympanal cavity is represented by a membranous bulge supported by a weakly sclerotized frame. In *Phyrganidia californica*, pocket I is modified and resembles a horizontal, lateral bridge (Fig. 6D). There is a hint of pocket III, and pocket IV is reduced. The tympanal cavity is extremely shallow, and the tympanal membrane is large (Fig. 6D). An external view of this tympanum is illustrated in Miller (1987). Illustrations of internal views of reduced dioptine tympana can be found in Richards (1932), Sick (1940), and Kiriakoff (1950a). I interpret the missing pockets as secondary reductions rather than as primitive absence because Dioptinae are a derived element within Notodontidae (Minet, 1983; Weller, 1989; Miller, 1991).
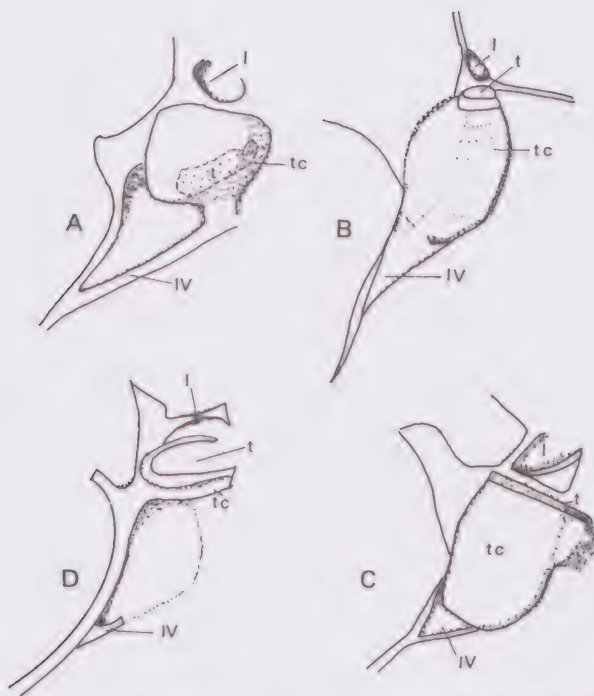
**Figure 6** Internal view of dioptine metathoracic tympana. A. *Scotura nervosa*; B. *Erbessa unimacula*; C. *Josia* sp; D. *Phryganidia californica*. I = pocket I, IV = open IV, r = pre-epimeral/epimeral ridge, t = tympanal membrane, tc = tympanal cavity.

I also examined one thaumetopoeine, *Thaumetopoea processionea*. It possesses a large, bowl-like tympanal cavity. Pocket I is represented by a slender bridge, pockets II and III are absent, and pocket IV is reduced (not figured). Whether pocket number and size represent secondary reduction or primitive absence is not known.

## Legs (Figures 7-8)

**Prothoracic Leg**. Modifications of the notodontid prothoracic leg are often sexually dimorphic, with androconial hairs (Table 5). In many Nystaleinae, males possess a prothoracic femur and tibia with modifications typical of pheromone production and dispersal (Figs. 7, 8). The lateral inner surface of the femur has one (e.g., *Bardaxima, Calledema*; Figs. 7B, 8A) or two (e.g., *Nystalea*; Fig. 8B) elliptical, slightly concave areas of membranous cuticle covered with woolly hairs and surrounded by flat, truncate scales with wide lamellae characteristic of androconia (McColl, 1969). Longer hairs overlay these shallow, glandular pockets. Near the proximal articulation of the tibia, a cluster or "pencil" of long scales occurs on a raised patch of cuticle. This pencil lays in a flattened
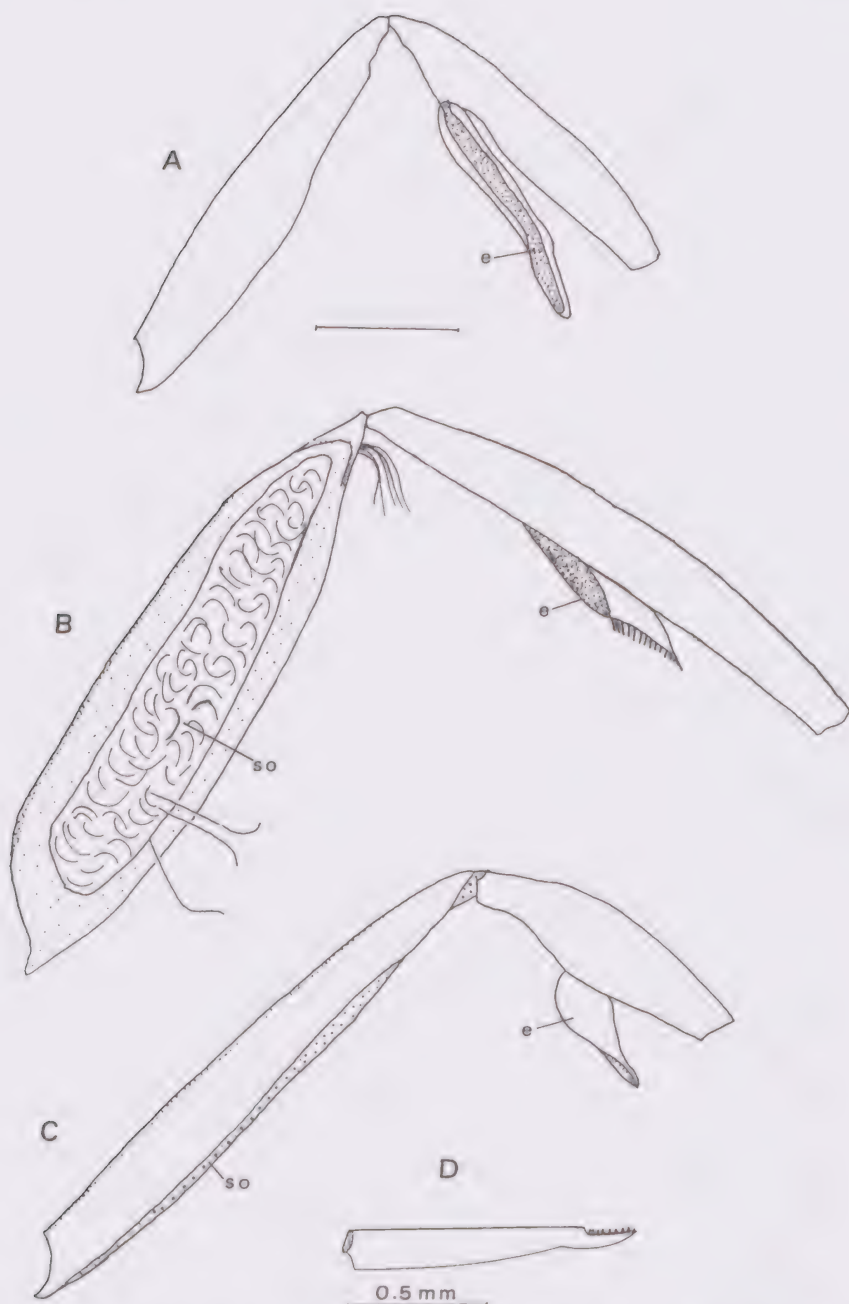
**Figure 7** Modifications of male legs. A-C. Prothoracic femur and tibia; A. *Urgedra striata* (normal condition); B. *Bardaxima* sp. (single pocket condition); C. *Apela* sp. (ventral femoral pocket condition); D. *Strophocerus cossoides*, male metathoracic tibial spur serrations. s.o. = putative scent organ, e = epiphysis. (Scale = 1.0 mm)
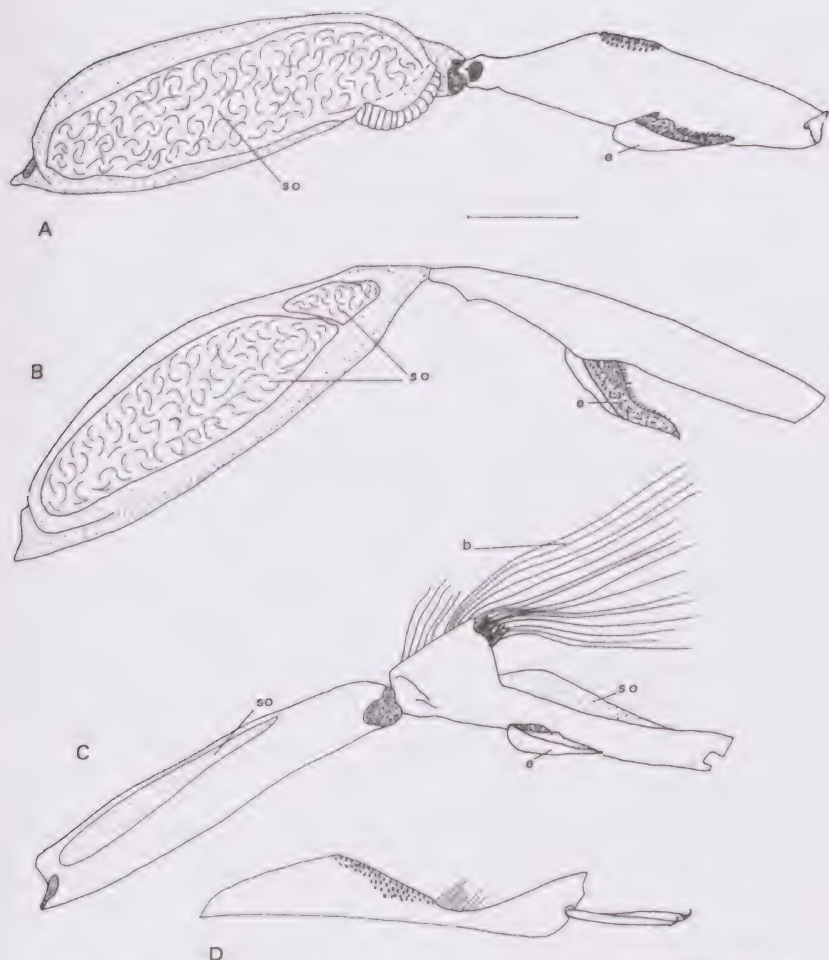
**Figure 8** Other leg modifications of males. A-C. Prothoracic femur and tibia; A.
*Calledema* sp. (single pocket); B. *Nystalea aequipars* (double pocket). C.
*Lysana plexa*; D. *Lysana plexa* (mesothoracic tibia). s.o. = putative scent
organ, e = epiphysis, b = distributing pencil. (Scale = 1.0 mm)

area or groove on the ventral, tibial surface, and extend to the first tarsal
segment in some species. In *Lysana plexa* Möschler, the surface under-
lying the tibial hair pencil is also membranous, and the pencil is very
large (Fig. 8C).

These femoral organs are analogous to the mesothoracic leg scent
organ in some male noctuids (Birch and Hefetz, 1987), and probably have
a similar function. Presumably, membranous areas produce short-range
pheromones that are distributed by the tibial scent pencil during court-
ship.

Other modifications of male prothoracic legs can occur. In some species
(e.g., *Apela* sp.: Hemiceratini, Fig. 7C), the femur's ventral edge is

Table 5. Male structures with putative courtship function in neotropical Notodontidae (Pt. = prothoracic, Ms = mesothoracic, Mt = metathoracic, s.s. = scent scales, s.h.= hair-like scent scales, s.p.= scent pencil, SSO = saccular scent organ)

| Location | Description | Examples |
|---|---|---|
| Pt femur | one glandular area | Bardaxima |
| Pt tibia | two glandular areas | Nystalea |
| Ms femur | s.h., s.s. or s.p. | Nystalea, Bardaxima |
| Mt tibia | s.h.,s.s. | Nystalea |
| Mt tibia | s.h., s.s. | *Hapigia curvilinea* |
| Hindwing | tibial spur gibbose | *Calledema marmorea* |
| Pleuron 3 and 4 | stigma | many *Hemiceras* |
| Sternum 4 | glandular area, s.h. | *Phedosia turbida* |
| | cteniophore | many Heterocampinae, *Hapigia* |
| Sternum 5 | peniculus | *Calledema marmorea* |
| Sternum 8 | cuticular brush | *Marthula pulchra* |
| | posterior edge | *Lyricinus* |
| Tergum 8 | s.h., s.s. | some *Dasylophia* |
| Sacculus | SSO: pleated, glandular, s.h., s.s. | many notodontids |
| Sacculus | Barth valve: sacculus enfolds s.p. | most *Hemiceras* *Hapigia* |

grooved and surrounded by scent hairs and scales. In *Hapigia* (Hemiceratini), the mesal surfaces of the femur have a single row of stout setae covered with scales (not shown), and long scent scales emanate from the proximal mesal and posterior edges of the coxae (Fig. 4a). Two scent pencils are associated with an enlarged, pleural membrane that enfolds their base (Fig. 4b: X). The furca, cervical sclerite and a ridge emanating from the proepimeron fuse above the coxa, and provide a reinforced, muscle attachment point (Fig. 4b: Q). The insertion points of the pencils are sclerotized. The scent pencil scales extend along the inner surface of the femur, and fan out when the legs are separated. A portion of the mesal coxal surface is modified into membranous cuticle covered with flat androconia (Fig. 4b: so, ss).

The notodontid epiphysis is usually one-third to one-fourth the length of the tibia, and has a comb of stiff setae (e.g., Nystaleinae, Hemiceratini, some Dioptinae and Heterocampinae), although it may be long and flattened with a rough surface (e.g., some *Dasylophia*, some heterocampines, Dicranurini and Thaumetopoeinae) (compare Figs. 7A-C; also Marumo, 1920). The tarsi are spinulose, and as in many Lepidoptera, there are usually two long tarsal setae on the distal end of

the fifth tarsomere (Oseto and Helms, 1976). Multiple (usually 4 to 6), long tarsal setae occur in several nystaleine genera (e.g., *Nystalea*, *Elymiotis* Walker, and *Bardaxima*), and number of setae can vary between sexes. Multiple, short tarsal setae occur in *Thaumetopoea processionea*. Tarsal claws on all legs may be single or bifid (= dentelées: Kiriakoff, 1950a; Weller, 1987, 1989, 1990; Miller, 1991), and their apices smooth or serrate (Janse, 1920; Arru, 1965; Weller, 1987, 1989, 1990, Miller, 1991).

**Mesothoracic Leg**. Usually the femur and tibia are unmodified, and the tibia and tarsomeres are spinulose. Mesothoracic tibiae have one pair of tibial spurs which often have serrations or comblike ridges on their apices (Janse, 1920; Miller, 1991; Fig. 7D). Such tibial spur serrations occur in many notodontids, but they are visible only under high magnifications. They occur in the Dioptinae, but not in *Gazalina* (Thaumetopoeinae). The same condition is found in *Lymantria* Hübner and *Dasychira* Hübner (Lymantriidae) (Miller, 1991).

**Metathoracic Leg**. In males, the femur and tibia have long hairs and scales arising from the caudal surface. These may disperse pheromones produced from structures on the abdomen (Jordan, 1923) or genitalia (below). There are usually two pairs of tibial spurs, again with tibial spur serrations, but one pair is lost in four unrelated lineages: Thaumetopoeinae, Dicranurini, some Dudusinae and some Heterocampinae (i.e., *Stauropus* Germar) (Miller, 1991). Again, tibia and tarsomeres are spinulose and tibial spurs often serrate.

## Wings (Figs. 9, 10)

Wing coloration in Notodontidae tends to be cryptic with subtle patterns (Draudt, 1932). Ground colors of brown or drab green are common, although Dicranurini wings are usually white with black markings. In fresh specimens of *Dasylophia* sp., the brown and black pattern is overlaid with light greens and pinks that give the forewing a lichen and moss covered appearance. These pigments are unstable and fade by the third year after a specimen has been collected. Wing coloration in Dioptinae ranges from gray (*Scotura* Walker) or brown (*Phryganidia* Packard) to bright, mimetic species (e.g., *Josia* Hübner) (Hering, 1925; Miller and Otero, 1994).

In females, number of frenular bristles tends to be constant within monophyletic lineages. The number of bristles is two in Nystaleinae (except *Lusura* with three), and three in Hemiceratini (except *Apela* with two) and Dioptinae surveyed. Number of bristles range from four to six in some Heterocampinae, to many (up to 20) in some Heterocampinae and Thaumetopoeinae (Arru, 1965; Miller, 1991).

Forewing venation sometimes varies within monophyletic genera (e.g., *Nystalea*), and this has led to splitting by workers who relied solely on wing venation to characterize genera. The forewing areole may be present or absent, and the position of veins R2, R5 and M1 can vary
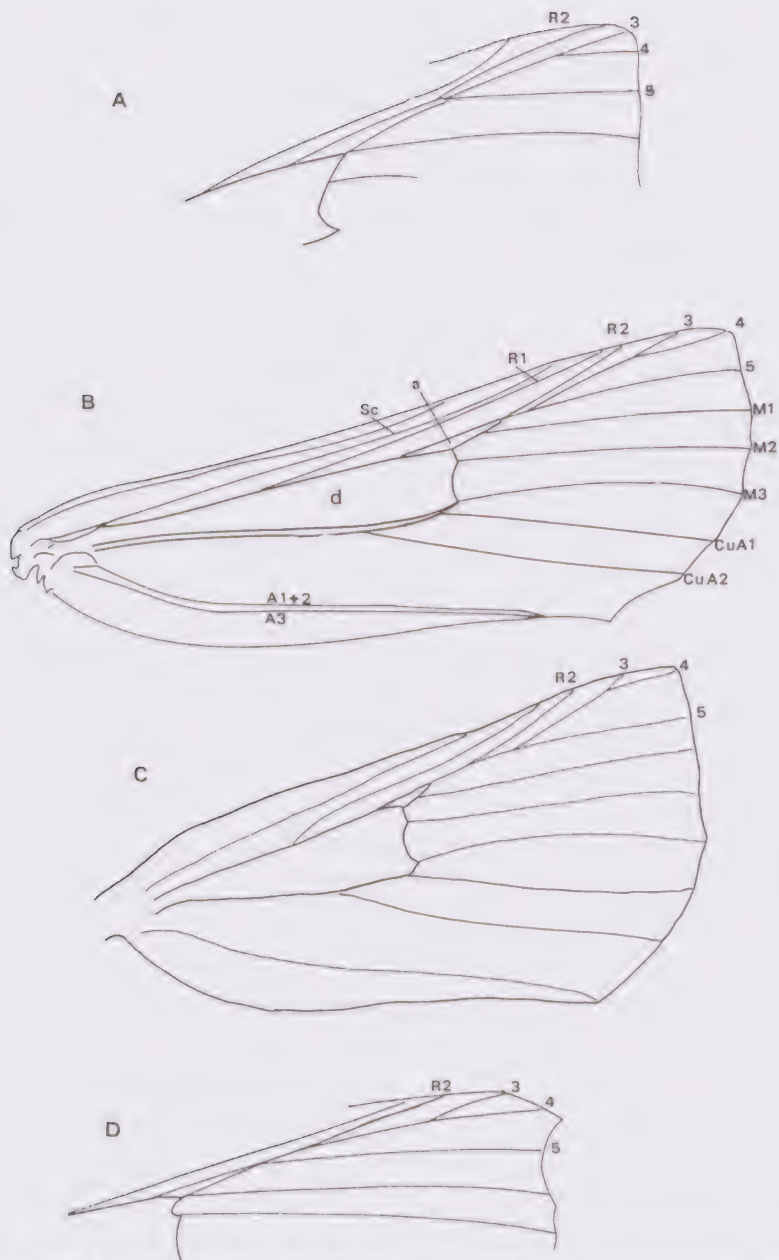
**Figure 9** Forewing veins. A. *Bardaxima lucilinea*; B. *Lysana plexa*; C. *Lyricinus xylophasioides*; D. *Calledema rufescens*. a = accessory cell, d = discal cell, Sc = subcostal vein, M1-M3 = medial veins, R1-R5 = radial veins, CuA1-CuA2 = cubital veins, A = anal veins.
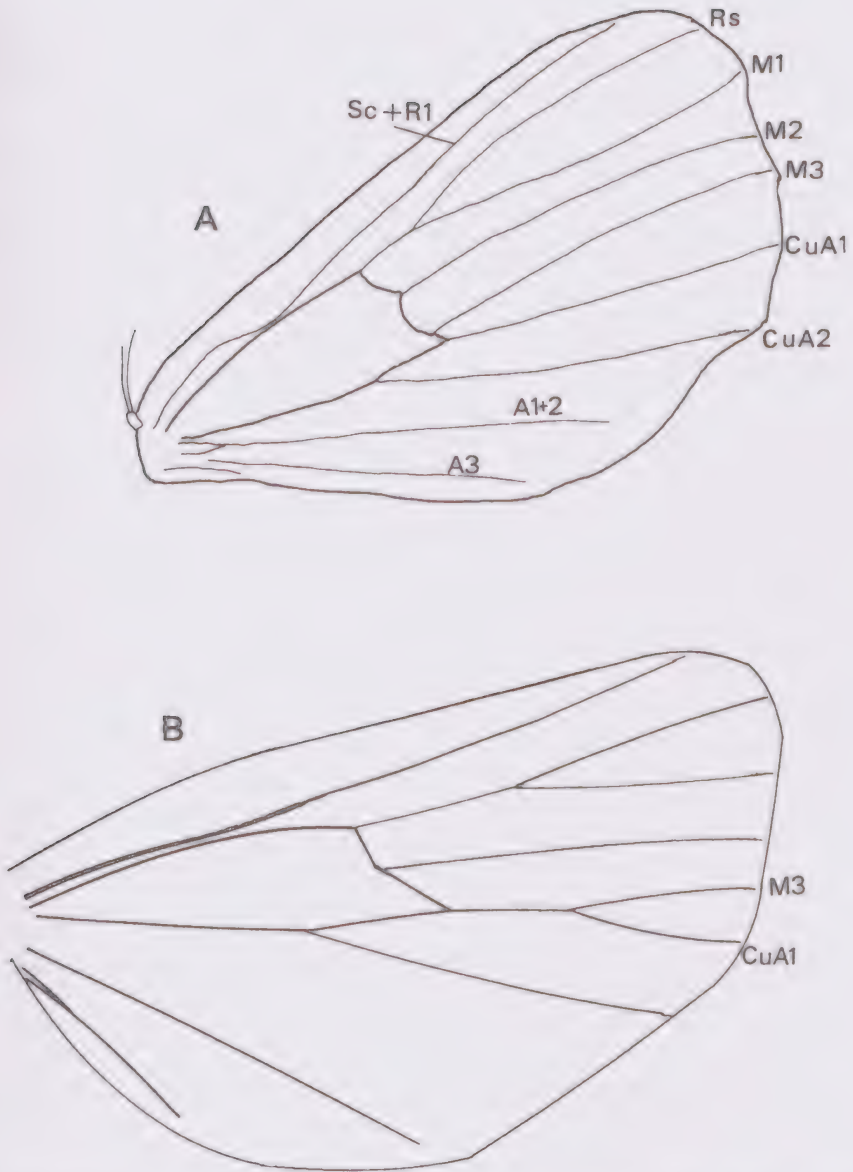
**Figure 10** Hindwing veins. A. *Marthula pulchra*; B. *Scotura nervosa*. d = discal cell, Sc+R1 = subcostal and R1 vein, M1-M3 = medial veins, RS = radial sector, CuA1-CuA2 = cubital veins, A = anal veins.

within genera (Fig. 9; Weller, 1989). Vein M2 usually arises from the midpoint of the discal cell or slightly above. In Dioptinae, M3 and CuA1 are usually stalked (Miller, 1987), a condition not found in other notodontids.

Hindwing venation in notodontids is less variable than forewing venation (Fig. 10). Veins Sc-Rs can be connate, short-stalked or long-stalked. Vein M2 arises from the middle of the discal cell except in *Hemiceras* and allies where the vein appears to have been lost. Veins M3 and CuA1 can be separate, connate or stalked. Again, multiple conditions can occur within monophyletic genera. In *Hemiceras* males, approximately two-thirds of the species (total = 150) have a small patch of specialized scales located on or near vein M3, termed a stigma by earlier authors (e.g., Schaus, 1901).

### Abdomen (Figs. 11-13)

Modifications of the male second abdominal sternum can occur, and both males and females may have structures for pheromone production and dispersal. Modification of the first abdominal segment is discussed under "Tympanum."

**Male**. The second abdominal (A2) sternum is usually simple with a faintly de-melanized, semicircular area anteriorly, here referred to as a "window" (Fig. 11A-D). The caudal border of the window is a flexion point. In some genera, these areas are translucent and elaborate (e.g., *Marthula*, *Elasmia astuta* [Schaus]) (Fig. 11C,D,F), and the cephalic edge is often reinforced. In *Antiopha*, this reinforcement is elaborated into a second set of apodemes (Fig. 11B, E).

The pleural region of A2 and A3 may be expanded with membranous or sclerotized outgrowths bearing hair-like scales (e.g., *Crinodes*: Dudusinae, *Phedosia*: Nystaleinae) (Fig. 12C). The cteniophore (Jordan, 1923) occurs on A4. It is a large flap with stout spines and internal levers for muscle attachment (Fig. 12A). The cteniophore is reduced in some species (e.g., *Heterocampa guttivitta*: Heterocampinae) and absent in most. On A5 of some *Calledema* sp. (Fig. 12B), a similar structure occurs. Thiaucourt (1985) named this structure the peniculus (latin: little tail, tuft) — not to be confused with "penicullus," a structure on the tegumen of noctuid male genitalia (Forbes, 1954). The peniculus, cteniophore and other modifications of abdominal pleura II and III appear to be serial homologues.

Tergum 8 may be modified externally with androconia (*Dasylophia* sp.; Fig. 13D), or modified internally for muscle attachments (Fig. 13A-C). Normally, its antecosta is present and well developed. Forbes (1916) showed that in the noctuid *Apamea amputatrix* (Fitch), genitalic retractor muscles (T1 and T2) extend from the eighth antecosta to the tegumen and vinculum. These retractor muscles are widespread in the Lepidoptera (e.g., Forbes, 1939b; Stekolnikov, 1967; Stekolnikov and Kuznetsov, 1986; Tikhomirov, 1979). In Nystaleinae and several addi-
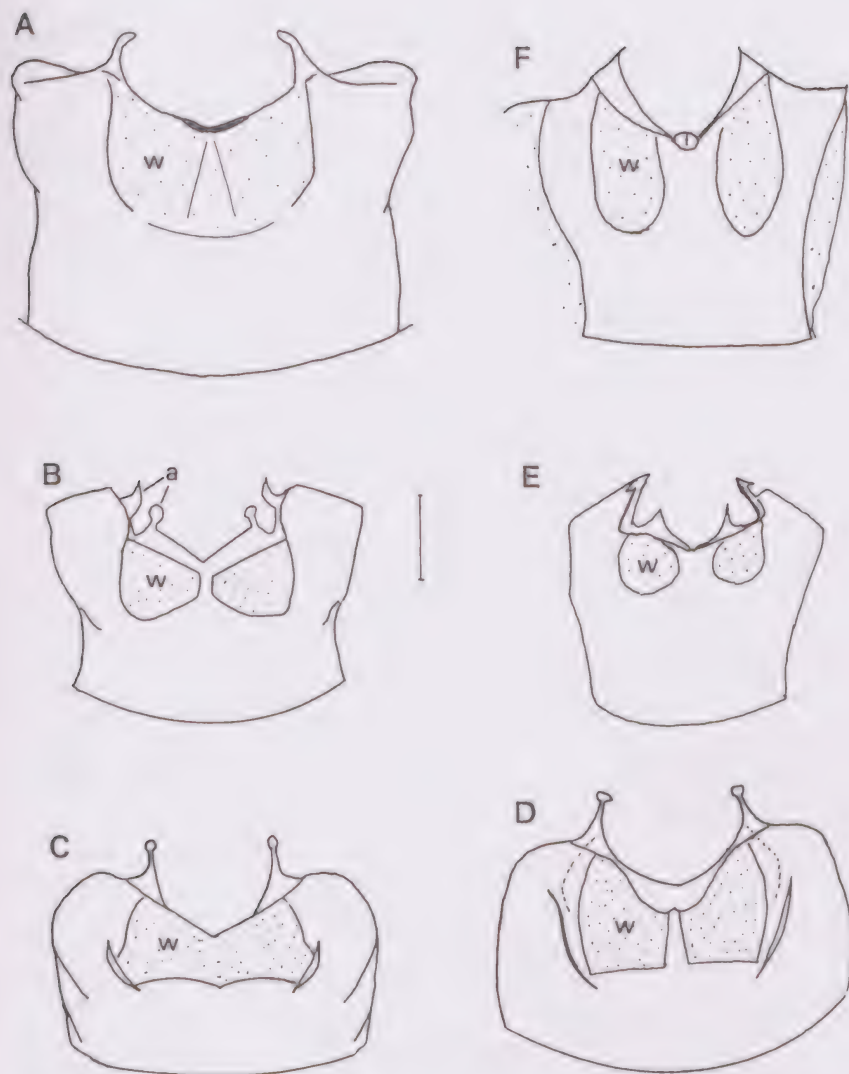
**Figure 11** Male second abdominal sternum. A. *Elasmia astuta*; B. *Antiopha discreta*; C. *Marthula pleione*; D. *Marthula griscesens*; E. *Antiopha multilinea*; F. *Kryptokalos cilla*. a = antecostal apodeme, w = window. (Scale = 1.0 mm)

tional neotropical genera, the antecosta is weak or absent. Tergum 8 is usually medially divided with either a mid-dorsal plate or paired ridges for muscle attachment (Fig. 13A-D). Presumably, the T1 and T2 muscles have shifted their insertion from the cephalic edge to the mid-dorsal region of the tergum in these species. This shift appears to be correlated
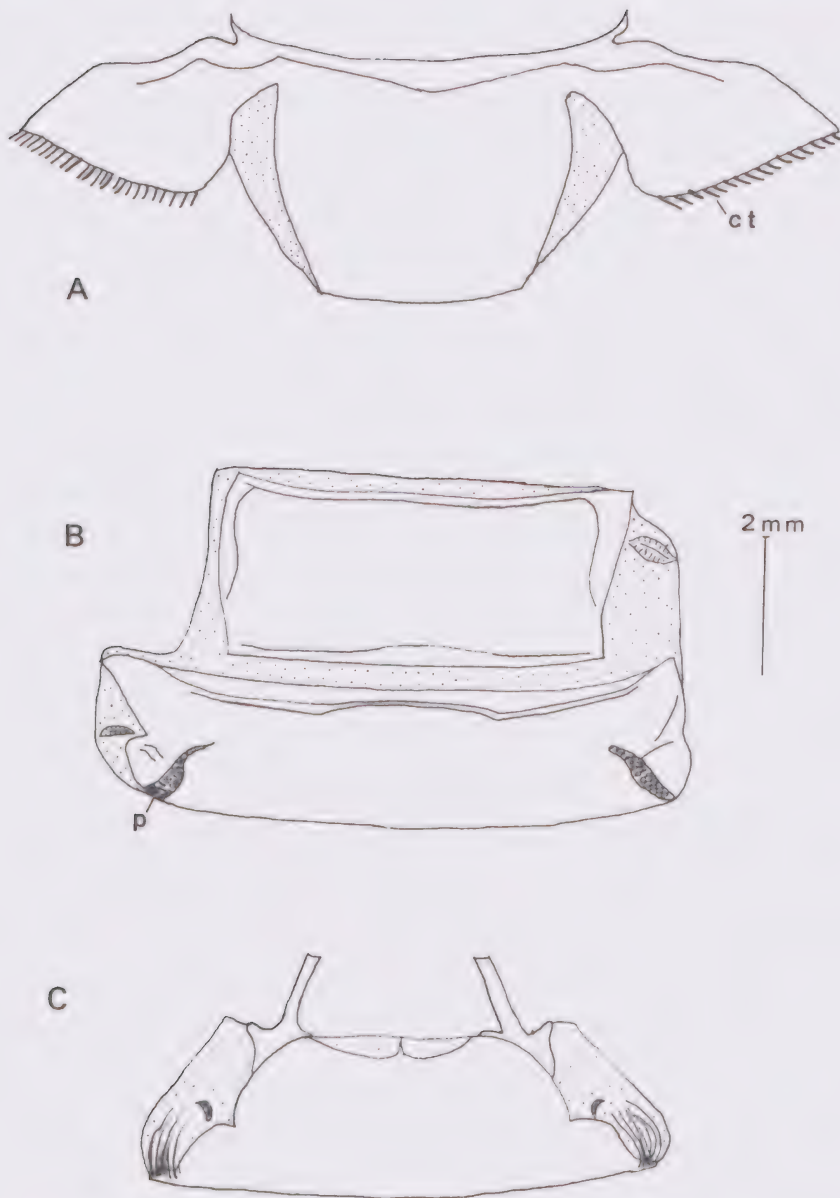
Figure 12 Male abdominal structures with probable courtship function. A. Sternum 4, cteniophore (*Hapigia* sp.); B. Sterna 4 and 5, peniculus (*Calledema jocaste*); C. Tergum 2 (*Lysana plexa*). ct = cteniophore, p = peniculus. (Scale = 2.0 mm)
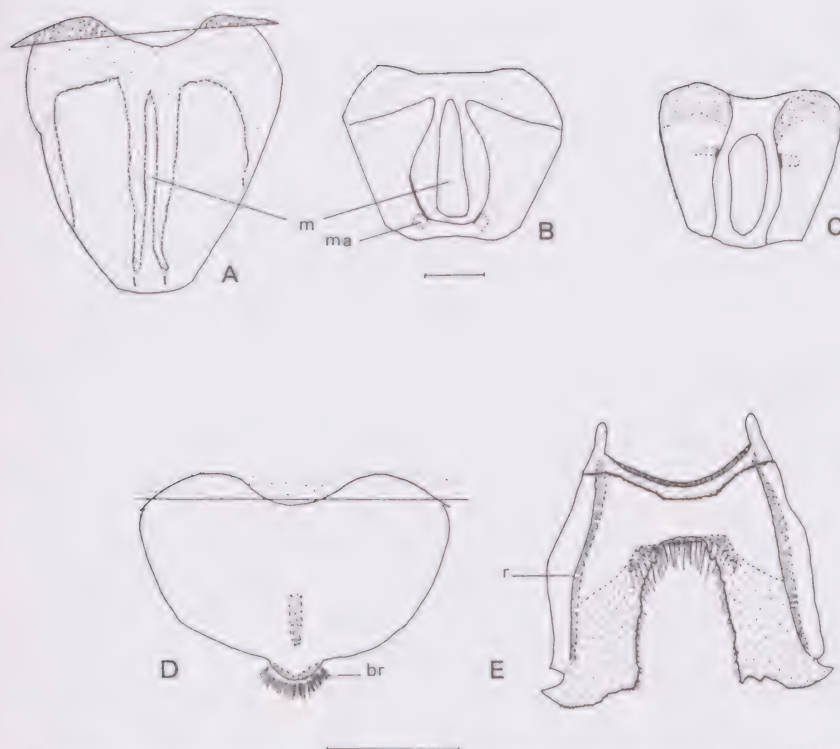
**Figure 13** Male eighth terga and parallel ridge condition of sternum 8 (anterior at top). A. Tergum 8 (*Ankale maonica*); B. Tergum 8 (*A. viridis*); C. Tergum 8 (*A. grammodes*); D. Tergum 8 (*Dasylophia* sp.); E. Sternum 8 (*Dasylophia* sp.). br = brush, m = midplate, ma = muscle attachment, r = internal ridge. (Scale = 1.0 mm)

with development of a long intrapleural membrane between the eighth segment and genital capsule (Miller, 1991).

Modifications of sternum 8 are often species- specific in Notodontidae (e.g., Franclemont, 1946; Forbes, 1948; Miller, 1987; Weller, 1990, 1992). Shape of the antecosta varies between and occasionally within monophyletic genera. In addition, hair-like androconia may be associated with membranous areas caudal to the antecosta. Such structures are found in some Phalerinae and Heterocampinae (Forbes, 1948). As in the tergum, lateral ridges and caudal structures of sternum 8 appear to provide sites for muscle attachment (Fig. 13E). Sternum 8 can bear a diversity of species-specific structures on the caudal edge. These range from a simple, glandular surface with hair-like scales (*Lepasta*, Fig. 14) to complex cuticular evaginations (*Marthula*, Fig. 15).

**Female**. Abdominal segments are rarely modified. Sternum 7 may have a patch of scent scales overlaying setae (e.g., *Dasylophia maxtla*
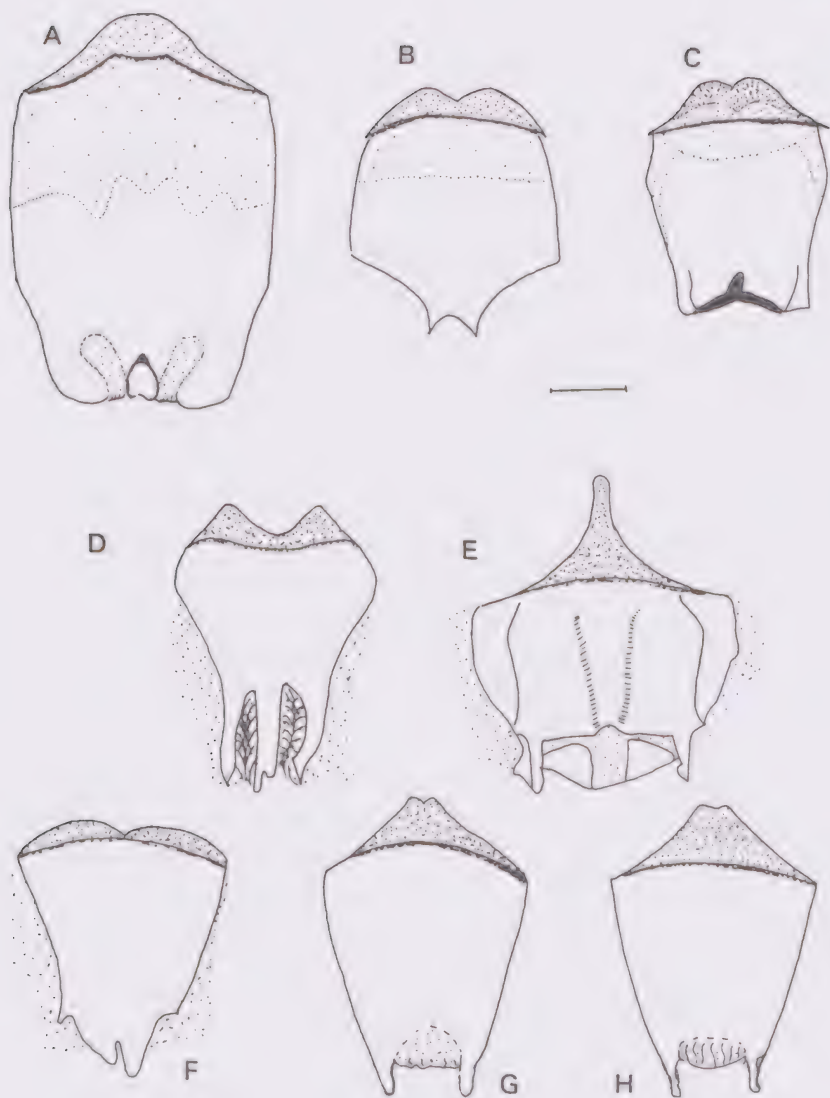
Figure 14 Male sternum 8 (anterior at top). A. *Ankale manacoides*; B. *A. viridis*; C. *A. maltha*; D. *A. maonica*; E. *Lepasta bractea*; F. *Antiopha* nr. *albosigma*; G. *Antiopha albosigma*; H. *Antiopha multilinea*. (Scale = 1.0 mm)

[Schaus]). In thaumetopoeines, sternum and tergum 7 form a continuous, lightly sclerotized ring that is covered with stiff deciduous hairs and scales. These scales may be a contrasting color (black or gold), and this "boule de laine" has been cited as a synapomorphy for the group (Kiriakoff,
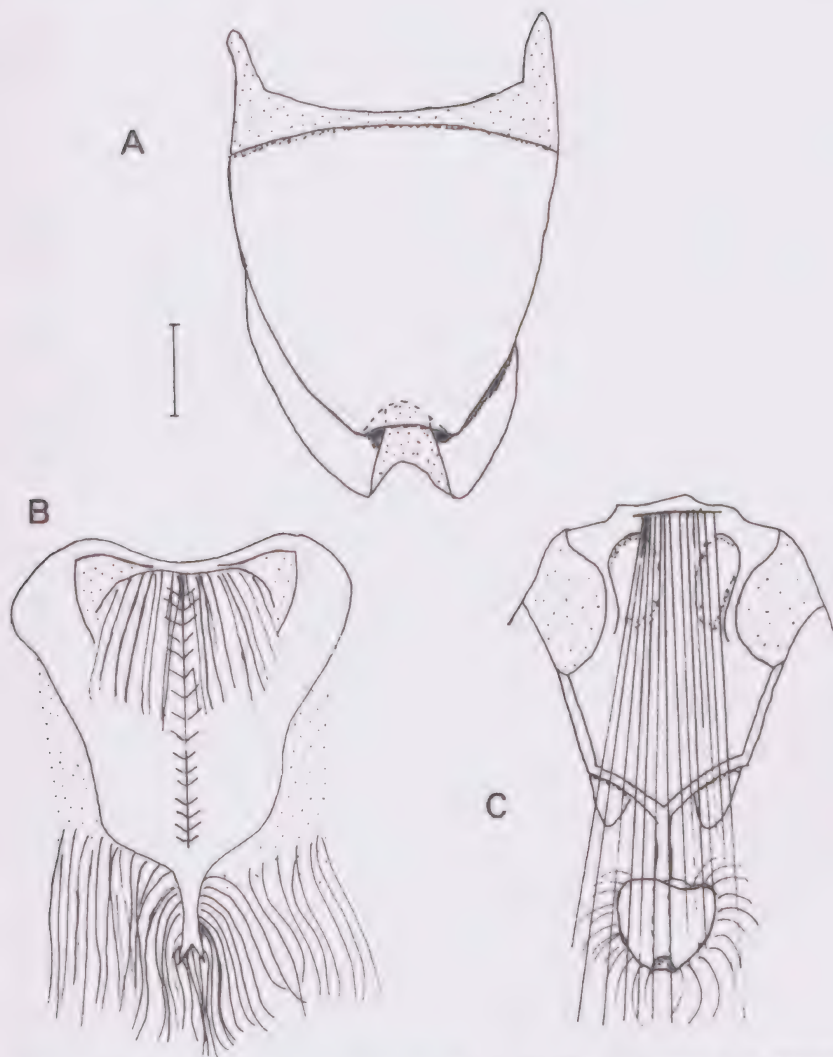
**Figure 15** Male sternum 8 (anterior at top). A. *Marthula grisescens*; B. *Marthula mumetes*; C. *Marthula pulchra*. (Scale = 1.0 mm)

1969). However, the same modification also occurs in females of *Lobeza* Herrich-Schäffer, a large, neotropical species (male wingspan 63 mm, female 91 mm). Male genitalia and the larva (BMNH) of *L. Smithi* Druce are characteristic of Heterocampinae, suggesting that the continuous seventh tergal-sternal ring has evolved independently in *Lobeza* and thaumetopoeines.

## Genitalia (Figs. 16-22)

Morphology of notodontid genitalia has been described (Forbes, 1948; Barth, 1955; Holloway, 1983; Miller, 1987, 1988, 1991 and references therein; Weller, 1990, 1991).

GENITALIA: MALE

**Tegumen and vinculum** (Figs. 16, 17). In Nystaleinae, the two halves of the vinculum are partially fused, and a sclerotized, caudal extension covers the base of the sacculus (Fig. 16). In most notodontids, the vinculum is rounded and the halves not fused.

When the tegumen and vinculum are fused, two nonhomologous conditions are found. In many neotropical notodontids, the tegumen-vinculum connection is fused in an S-shaped configuration (Fig. 16B). The other condition is typified by the holarctic genus *Pheosia* (Notodontinae). Here, the tegumen and vinculum form a single, fused C-shaped structure (Fig. 16D) presumably to support massive valves that articulate with it.

The uncus-tegumen juncture varies extensively (Fig. 17). The uncus and tegumen are sometimes completely fused, and have reinforcing, internal apodemes extending from the uncus into the tegumen (Fig. 17C,D). Apodeme shape and degree of fusion also varies. Apodemes may be absent, in which case the uncus base connects to the tegumen by a hinge of pleural membrane (e.g., *Calledema rufescens* Schaus). Usually, the tegumen-uncus connection is characteristic for a genus, but within *Calledema*, several configurations exist.

Uncus shape may or may not be characteristic for a genus. In some nystaleine genera, the distal process becomes membranous and setose (e.g., *Elymiotis, Poresta*). In some *Nystalea*, the distal process is curved and thin with an enlarged tip (Figs. 16A-C).

Above the anal tube and tegumen-uncus suture, paired, setose structures articulate on the venter of the uncus in Nystaleinae and many other notodontids (Figs. 16, 17). Kiriakoff called these structures gnathi (e.g., Kiriakoff, 1981), but Kiriakoff's use of the term is inconsistent with both Pierce (1914) and common usage. Pierce described the gnathos as a "free ring, enclosing the anus," and reserved the term socii for hairy pads arising from the base of the uncus. Forbes (1923) applied the term gnathos to part of the subscaphium located below the anal tube. Klots (1970), following Pierce, suggested that the gnathos is derived from the caudal edge of the uncus and glabrous, whereas socii were derived from the uncus base and setose. In several notodontid species, these setose structures are fused to the base of the uncus (e.g., Phalerinae). The term socii appears to be most appropriate for these structures.

**Valve** (Figures 16, 18, 19). The valve in many species of neotropical notodontids (e.g., some Heterocampinae, most Nystaleini (sensu Miller, 1991), *Pentobesa*, many Dioptinae and Hemiceratini) have a membranous, highly pleated sacculus (= corrugated sacculus; Holloway, 1983)
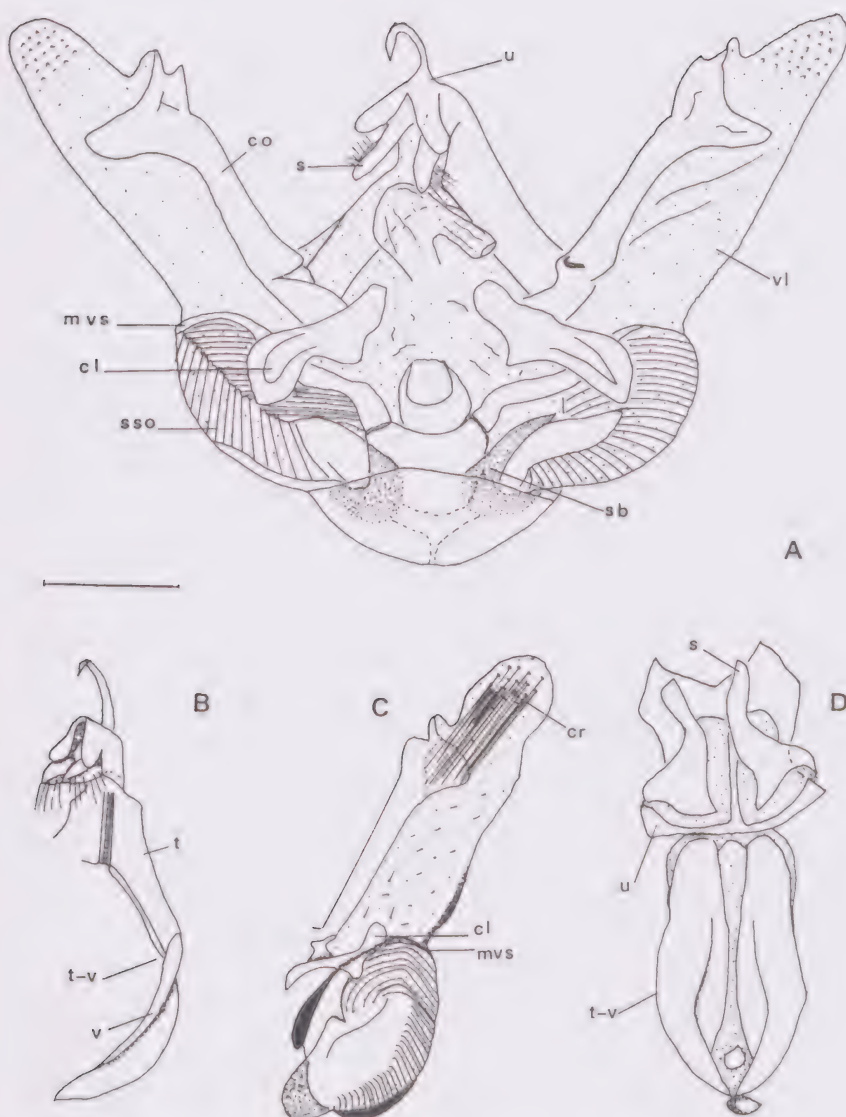
Figure 16 Male genitalia. A. *Nystalea aequipars*;  B. caudal view of tegumen, vinculum and sociuncus of *Nystalea virgula*, valve removed; C. right valve of *Nystalea virgula*; D. *Pheosia tremula*, valvae removed. cl = costula, co = costa, cr = coronalike structure, mvs = midvalve sclerotization, sb = sclerotized base of sacculus, s = socius, sso = saccular scent organ, t = tegumen, t-v = tegumen-vinculum junction, u = uncus, v = vinculum, vl = valvula. (Scale = 1.0 mm)
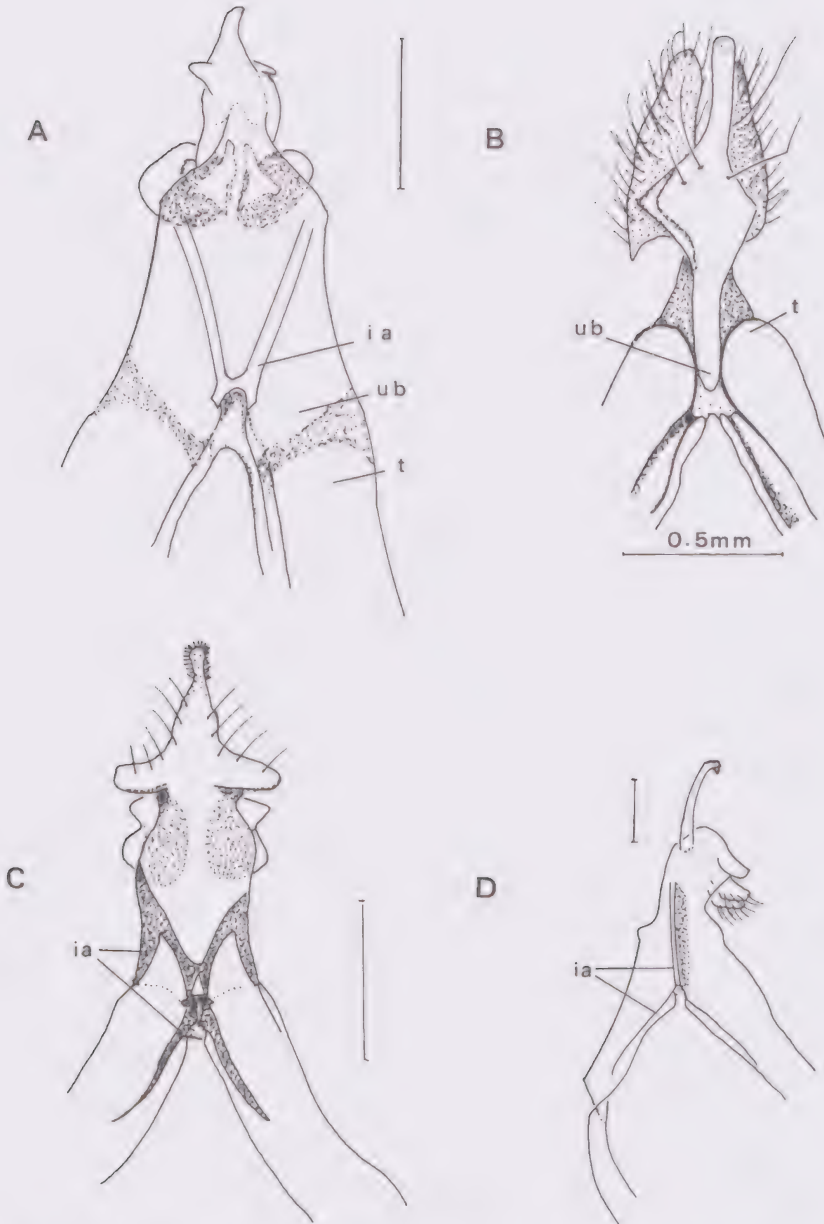
**Figure 17** Dorsal view of uncus-tegumen attachment. A. *Elymiotis ancora*; B. *Gopha mixtipennis*; C. *Poresta joanna*; D. *Nystalea aequipars*. ia = internal apodemes, t = tegumen, ub = uncus base. (Scale = 1.0 mm)

(Fig. 16). A mix of long hair-like and spatulate scales arises from its base. Barth (1955) demonstrated that a gland is located within the sacculus of *Hemiceras proximata* Dognin, and suggested that it produces phero- mones. I refer to the pleated sacculus with associated hairs as the **saccular scent organ** (SSO) (Weller, 1989, 1990). Although pheromone producing organs and androconia are often associated with male genita- lia (e.g., coremata of Arctiidae), this is an unusual example of the primary genitalic structures being themselves pheromone-producing. Typically, a sclerotized band separates the SSO from the rest of the valve. This midvalve sclerotization (Weller, 1990) appears to divide the valve into costal and saccular compartments. This sclerotization can be expanded as in *Pentobesa* or *Bardaxima*. Occasionally, the midvalve sclerotization is reduced and the SSO is not distinct from the remainder of the valve (e.g., *Lysana plexa*: Nystaleinae; *Disphragis tharis*, *Rifargia lineata*: Heterocampinae). In these, the flattened SSO does not expand as greatly. In some species, a modified saccular base occurs in the presence of an SSO. Here, a small hook or ridge is present that presumably provides an anchor for the valval flexor muscles (M5: Forbes, 1939b; Tikhomirov, 1979).

The SSO is variously developed within and between genera. It can be greatly enlarged as in *Marthula* and many Dioptinae. In some species of the Hemiceratini (e.g., *Hapigia*, most *Hemiceras*), the sacculus is greatly elaborated and enfolds a large scent pencil (Fig. 18). I refer to this



Figure 18 Male genitalia of *Hemiceras constellata* showing the Barth valve. A. Genitalia with right valve removed; B. Right valve. B = Barth valve (= sacculus), co = costa, vl = valvula.
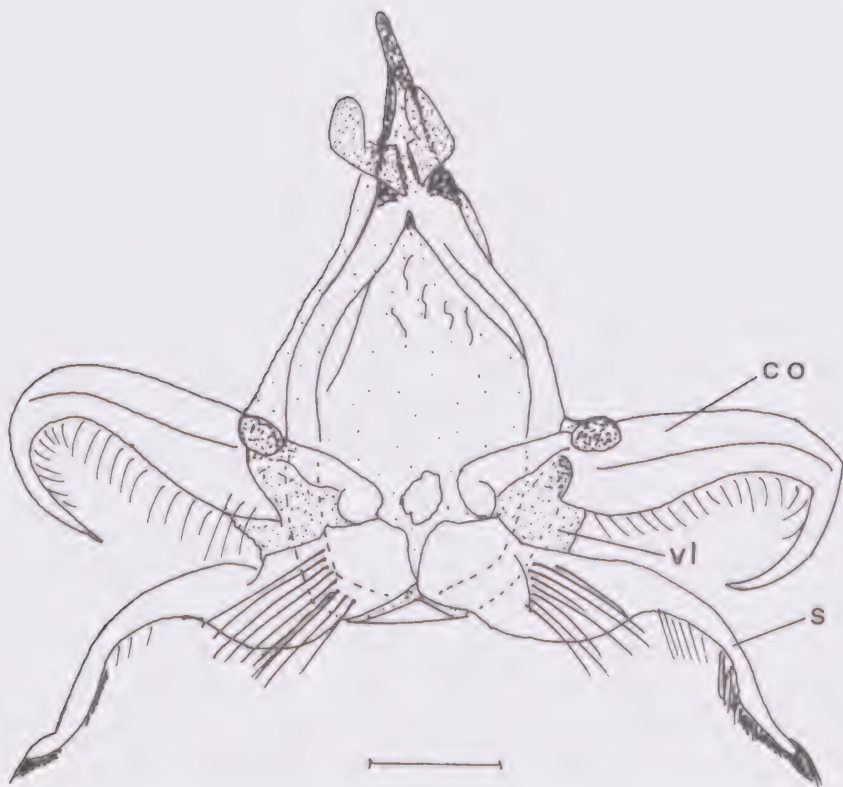
**Figure 19** Male genitalia of *Dasylophia colimata.* co = costa, s = sacculus, vl = valvula.
(Scale = 1.0 mm)

complicated SSO as the Barth valve, in honor of Dr. R. Barth and his pioneering studies on the Brazilian fauna.

The SSO can also be reduced in a variety of non-homologous conditions. In *Pentobesa* and some members of the *Dasylophia*-group, the SSO is usually moderately developed, the pleats are less numerous than in nystaleines, and the sacculus is smaller. Pleats are completely absent in some representatives of the *Dasylophia*-group, and the sacculus is sclerotized (e.g., *D. colimata* Dyar, Fig. 19).

In many notodontids, the costa is a massive structure with various projections along its length. These are uncommon in Nystaleinae. The costa of nystaleines is usually a thin, sclerotized rod that may or may not extend completely to the apex of the valve. In *Nystalea*, the dorsal edge is sclerotized for two-thirds the length of the valve and widens into a characteristic shape (Figs. 16A, 16C). Beyond this widening, the distal portion is membranous with short setae and stiff hairs analagous to a noctuid corona (Forbes, 1954).

In nystaleines, some hemiceratines, and some heterocampines, a sclerotized process arises proximally from the dorsal edge of the costa, and extends into the anellus. Muscle attachments occur at its base (Fig. 16). Presumably, these structures, in conjunction with the socii, uncus and costa, provide traction in copula. Forbes (1948) suggested that these processes might be homologous with structures in the geometrid genera *Himera* Duponchel and *Nacophora* Hulst, and with the hairy pads of Thyatiridae. From limited observations, I conclude that the processes in these three families are not homologous. I refer to this structure as the **costula** (Latin: little rib) (Weller, 1990), distinguishing it from the costal process of the sacculus (Forbes, 1954). The costula appears to be a modification of the noctuoid transtilla, and its shape is usually species-specific. Dioptines lack costulae, and instead have a fused transtilla that arises from the base of the costa (Miller, 1991).

A membranous region occurs between the sclerotized costa and midvalve sclerotization in nystaleines. This region varies from being slightly to extremely pleated (*Bardaxima*), and has scattered setae or patches of setae and hairs (Figs. 16A, 18). It appears to be homologous with the valvula of Pierce (1914) (Weller, 1990).

**Anellar Region**. The anal tube is often weakly sclerotized ventrally in thin vertical strips. Ventral to the costulae, scattered setae occur. The juxta is sclerotized and varies from slightly to extremely concave in nystaleines. In other notodontids, the dorsal edge of the juxta may be elaborated into an aedeagus guide or stabilizer (e.g., *Lirimiris*).

**Aedeagus** (Fig. 20). In Nystaleinae, the vesica (= endophallus; Klots, 1970) tends to be bulbous, terminating in a narrow tube that is directed cephalad. Deciduous cornuti, present in many genera, vary in size and shape (Forbes, 1948; Holloway, 1983).

Many modifications of the aedeagus occur (Fig. 20A-E). The distiphallus may have long processes (*Symmerista*) or small flanges (*Notela*). The basiphallus can be shovel-shaped (Fig. 20E) or tubular (Fig. 20C). Often, a ventral sclerotized piece occurs on the basiphallus that may provide extra surface area for muscle attachment. I call this an **aluta** (Latin: shoe of soft leather). This structure, which is attached to the manica, can be flat and sheetlike, caecum like, or bowl-shaped (Fig. 20D).

The aluta of *Nystalea* and related genera is an enlarged, tubular structure that has a characteristic triangular exit for the ductus seminalis (Fig. 20A, B). Large muscles attach both dorsally and ventrally (Weller, 1989, 1990; Miller, 1991). The term **callosum** (Latin: hard skin; Weller, 1990) has been used to refer to this specialized aluta, and it only occurs in Nystaleinae (Weller, 1989; Miller, 1991).

GENITALIA: FEMALE (FIGS. 21, 22)

Notodontid female genitalia show greater morphological variation than is usually found in the Noctuoidea, and it is not uncommon for them to be species-specific (Weller, 1992). However, within species complexes,
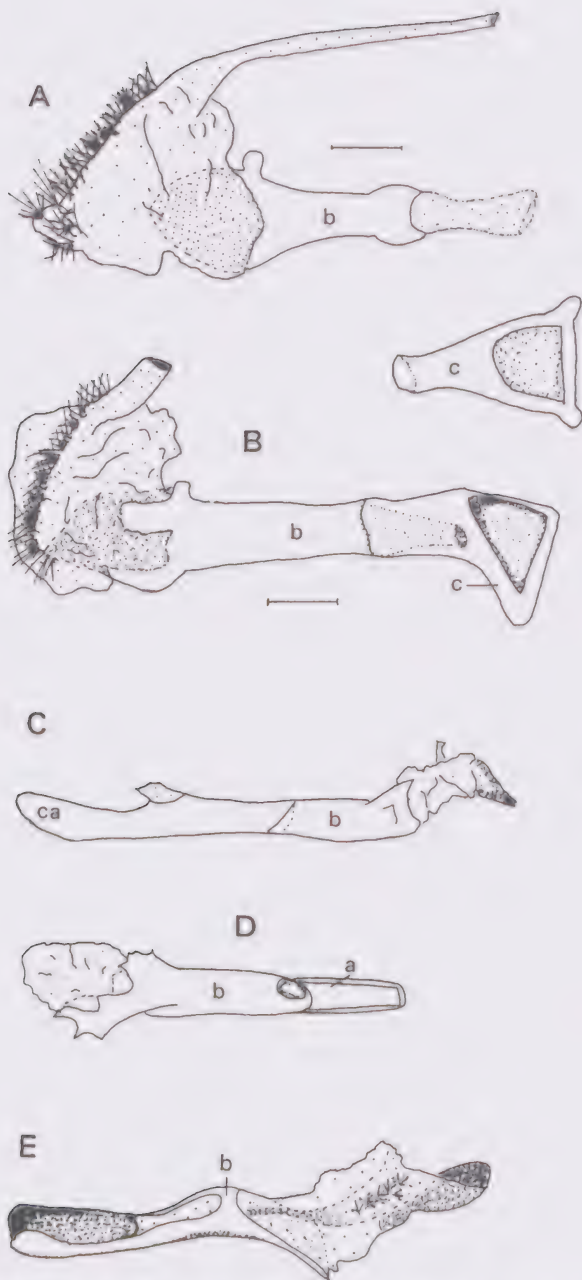
**Figure 20** Aedeagii. A. aedeagus with callosum removed (*Nystalea similis*); B. callosum (*Nystalea aequipars*); C. caecum (*Hemiceras* sp.); D. caecum with aluta (*Nadata gibbosa*); E. plain tube with aluta (*Rifargia lineata*). a = aluta, b = basiphallus, ca = caecum, c = callosum. (Scale = 1.0 mm)
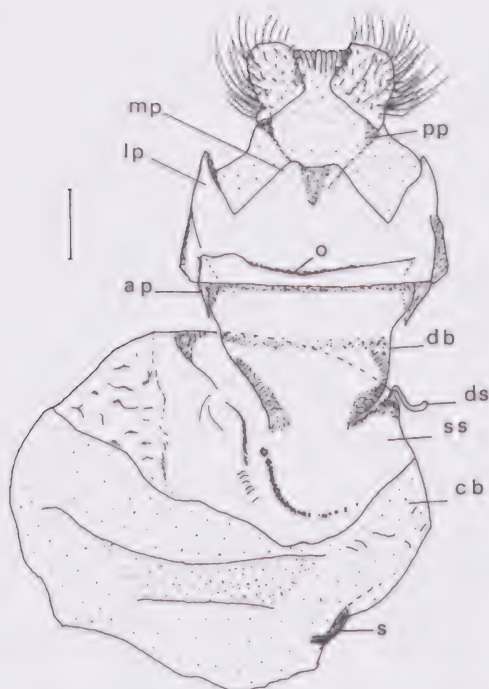
**Figure 21** Female genitalia of *Nystalea aequipars* (ventral view). ap = anterior apophysis, cb = corpus bursae, db = ductus bursae, ds = ductus seminalis, lp = lateral prominences on eighth sternum, mp = midventral prominence, o = ostium bursae, pp = posterior apophysis, s = signum, ss = sclerotized shield. (Scale = 1.0 mm)

female structures (e.g., lamellae antevaginalis, tergum 8) tend to have similar shapes (e.g., *N. aequipars* species complex; Weller, 1990).

**Ovipositor Lobes**. The papillae anales are usually membranous, but may be lightly or heavily sclerotized. In Nystaleinae, they are usually covered with short, scattered setae with longer, inwardly curved setae arising from the base. The lobes may be flattened and covered with stout, curved setae (e.g., *Notoplusia*, *Lyricinus xylophasioides*). In *Apela* Walker (Hemiceratini), the ovipositor setae resemble shepherd crooks. Ovipositor lobes of the neotropical heterocampine *Rhuda dimidiata* are concave, and the setae are long and curved with wide, spatulate tips. Other species of *Rhuda* have unmodified setae.

In nystaleines, posterior apophyses are typically long and slender, although they can be short and stout (e.g., *Calledema rufescens*). In *C. rufescens*, a sclerotized invagination is located dorsally between the papillae anales and tergum 8 (T8). Presumably, this invagination is associated with a pheromone gland.

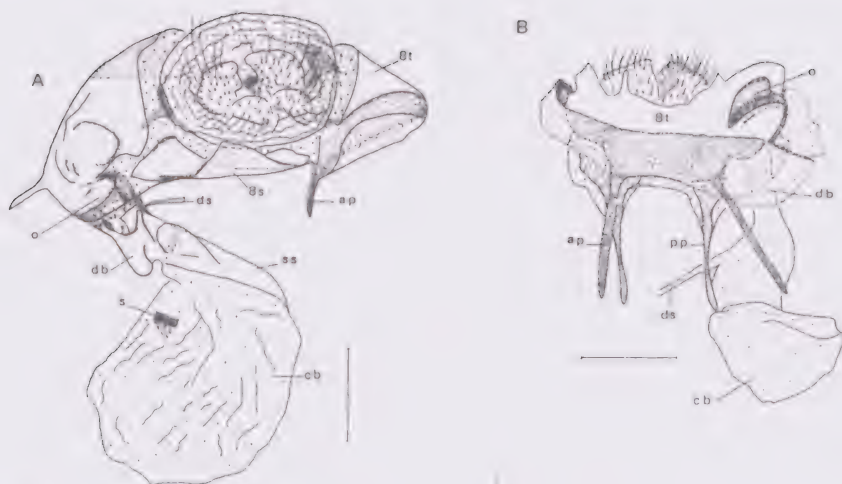**Sclerites of the Eighth Abdominal Segment**. The shape of T8 and

**Figure 22** Asymmetrical female genitalia. A. ventral view, *Dasylophia maxtla*;  B. dorsal view, *Pentobesa poecila*. ap = anterior apophysis, cb = corpus bursae, db = ductus bursae, ds = ductus seminalis, o = ostium bursae, s = signum, ss = sclerotized shield, 8t = eighth tergum, 8s = eighth sternum. (Scale = 1.0 mm)

S8 varies within and between nystaleine genera. Some species possess lateral processes on only the sternum or on both sternum and tergum. Some have additional lateral processes on the lamellae antevaginalis. The ostium bursae is usually very wide, extending nearly the entire width of S8 (Fig. 21). Some females have asymmetrical genitalia, and in these, the ostium bursae is usually located left of center. Asymmetrical genitalia are common in *Pentobesa* and the *Dasylophia terrena*-species group. In *Pentobesa poecila* (Felder), the ostium bursae is dorsal, located on the enlarged, distal edge of the apophysis (Fig. 22A). In *Dasylophia maxtla* (Schaus), the left anterior apophysis is reduced, and the ostium is located slightly ventral to the apophysis (Fig. 22B). The male genitalia in these species are also asymmetrical. Asymmetrical female insect genitalia are rare (reviewed in Eberhard, 1985). The ostium bursae of many notodontid females have various structures covering or blocking it (e.g., *D. anguina* [Smith], *Gopha mixtipennis*, *Heorta roseoalba*: Heterocampinae).

   **Other Structures**. The ductus bursae may be membranous, partially or completely sclerotized. In nystaleines, it is often sclerotized and dorsoventrally flattened (Fig. 21). In this case, the lateral margins are membranous, allowing them to expand into a rounded tube. The ductus bursae may be extremely short (e.g., *D. anguina*) or extremely long (e.g., *Hapigia* spp.: Hemiceratini), two to three times the length of the corpus bursae.

In Nystaleinae, the ductus seminalis often arises from the left ventral area of the corpus bursae (Fig. 21). However, it may also arise from near the ostium bursae, from the ductus bursae (Fig. 22) or from other areas of the corpus bursae. The corpus bursae itself may or may not be partially sclerotized. Where ductus and corpus bursae meet, there may be internal spinules or other modifications as in *Pentobesa lignicolor* Möschler or *Marthula mumetes* where a "necklace" of spines surrounds the mouth of the corpus bursae. Single or multiple signa are present, and their shape may be species-specific.

Summary of Morphological Trends

Although the morphology of Nystaleinae and other notodontids is difficult to characterize, certain trends can be noted. Mouthpart structures tend to be well developed in neotropical species and reduced in nearctic species. As in many Lepidoptera, female antennae are usually simpler than male. The prothorax usually has parapatagia; occasionally an additional lateral pair occurs. The tympanum may have all four pockets, with the fourth characteristically being "open," that is, with anterior and posterior struts not connected by a sclerotized sheet. Loss or reduction of pocket II is frequent in notodontids, and pocket III has been lost in all dioptines examined. Further tympanal reduction occurs in some dioptines and thaumetopoeines.

Species can often be assigned to genera based on female genitalic structures, but the diversity of both female and male genitalia makes generalizations difficult. When other tribes and subfamilies are more thoroughly surveyed, statements on genitalic trends in the family may be possible.

Several types of previously undescribed sexually dimorphic structures occur on male legs, wings, abdomen and genitalia in neotropical notodontids. Some species have androconia and glandular areas on both legs and genitalia (many nystaleines), on both pre-genital abdominal segments and genitalia (*Marthula*, *Hapigia*), or on all three areas (*Calledema*). The cteniophore is the only structure previously surveyed that has been ascribed a possible courtship function (McColl, 1969). A survey of these structures with more rigorous characterization of their function should be undertaken in light of these findings.

Summary of Morphological Terms and Synonyms

*Aluta* (new term)(Fig. 19D): sclerotized piece of cuticle attached to the ventral surface of the basiphallus. May have originated as an extension of the manica. Found in most notodontids.

*Anterior branch pocket* (new term)(Fig. 5): small pocket ventral to the tympanic cavity formed from an extension of the anterior branch of pocket IV. Found in some *Hemiceras* and some nystaleines.

*Barth valve* (new term)(Fig. 17): valve with sacculus enfolding a hair

pencil that emanates from the saccular base. Associated gland occurs within sacculus. Found in *Hapigia* and most *Hemiceras*.

*Callosum* (Weller, 1990)(Fig. 19A, B): specialized aluta enclosing the basiphallus, usually with a footlike projection. Unique to Nystaleinae.

*Costula* (Weller, 1990)(Fig. 15): sclerotized process arising from the base of the male valval costa. Occurs in nystaleines, some heterocampines and hemiceratines, and appears to be a modification of the noctuoid transtilla.

*Epimeral pocket* (new term)(Fig. 5): small pocket located on the pre-epimeron/epimeron suture of the metathorax. Found in some nystaleines, hemiceratines and heterocampines.

*Epimeral ridge* (new term)(Fig. 5) (= "le support anterior" of Kiriakoff, 1950a, 1950b, 1950c): an internal ridge located at the pre-epimeron/ epimeron suture of the metathorax that extends anteriorly from the tympanic cavity. Found in some nystaleines, hemiceratines and heterocampines.

*Midplate* (Weller, 1990)(Fig. 13): sclerotized area, sometimes with ridges, located in the middle of the male eighth tergum. Occurs in many notodontids.

*Midvalve sclerotization* (Weller, 1990)(Fig. 15): ribbonlike or expanded plate of sclerotized cuticle located on the inner mesal surface of the male valve, demarcating the dorsal edge of the sacculus. Occurs in many nystaleines, hemiceratines and dioptines. Usually associated with a pleated sacculus.

*Peniculus* (Fig. 12B, 13)(Thiaucourt, 1985): similar to a cteniophore, but pleural expansion is reduced. It occurs on male abdominal sternum V in *Calledema rufescens*.

*Pleural hood* (Fullard, 1984): expanded pleural membrane that surrounds the first abdominal spiracle, and cups the tympanal opening. Analogous to the noctuid tympanal hood. Occurs in *Hapigia* and *Antaea*.

*Pocket IV* (Richards, 1932)(Figs. 5, 6) (= "le support posterior" of Kiriakoff, 1950a, 1950b, 1950c): tympanal pocket located ventral to the tympanal cavity that is usually "open" with an anterior and posterior ridge defining its location. Anterior ridge reduced or absent in some notodontids (Kiriakoff, 1950a,c). Pocket IV has its opening towards the tympanal cavity when a sclerotized sheet connects the anterior and posterior supports (= "closed" condition). This pocket occurs in many notodontids.

*Saccular scent organ* (Weller, 1990)(Fig. 15): membranous and pleated sacculus with scent scales emanating from the base. Found in numerous neotropical (Weller, 1989) and asian species (Holloway, 1983).

## LITERATURE CITED

ARRU, G. M. 1965. *Pygaera anastomosis* (L.) (Lepidoptera, Notodontidae), studio morfologico ed etologico. Bol. Zool. Agric. Bachic. 1964-65: 207-271.

Barth, R. 1955. Maennliche Duftorgane Brasilianischer Lepidopteren 10. MITTEILUNG: *Hemiceras proximata* Dogn. (Notodontidae). Anais Acad. Brasil. Cienc. 27:537-545.

BIRCH, M.C. & A. HEFETZ. 1987. Extrusible Organs in Male Moths and Their Role in Courtship Behavior. Bull. Entomol. Soc. Amer. 331:222-229.

BLUM, M.S. 1981. Chemical Defenses of Arthropods. Academic Press, New York.

BOURGOGNE, J. 1951. Ordre des Lépidoptères. pp. 173-448 in P. Grassé, ed./ Traite de Zoologie, X, Fascicle 1, Masson, Paris, 975 pages.

BROCK, J.P. 1971. A Contribution Towards an Understanding of the Morphology and Phylogeny of the Ditrysian Lepidoptera. J. Nat. Hist. 5:29-102.

BUTLER, A.G. 1878. On the Lepidoptera of the Amazons, collected by Dr. James W.J. Trail, during the years 1873-1875. Part 2. Trans. Entom. Soc. London 1878:64-72.

DOGNIN, P. 1908. Hétèrocères Nouveaux de l'Amerique du Sud. Ann. Soc. Entom. Belg. 52:153-179.

———. 1909. Hétèrocères Nouveaux de l'Amerique du Sud. Ann. Soc. Entom. Belg. 52:74-94.

DOUBLEDAY, E. 1841. Characters of three new genera of Notodontidae, from North America. Entomologist 1:55-60.

DRAUDT, M. 1932. Notodontidae. pp. 905-1070 in A. Seitz ed./ Die Gross-Schmetterlinge der Erde. Die Gross-Schmetterlinge des Amerikanischen Faunengebeites. Vol. 6. Die Amerikanischen Spinner und Schwaemer. Alfred Kernen, Stuttgart.

DRUCE, H. 1890. Descriptions of New Species of Lepidoptera Heterocera from Central and South America. Proc. Zool. Soc. 1890:493-520.

——— 1891. Lepidoptera Heterocera: Family Notodontidae. Biol. Centrali-Americana, 2:452-469.

——— 1911. Description of Some New Species of Heterocera, chiefly from Tropical South America. Ann. Mag. Nat. Hist. (Series 8) 8:138-150.

DYAR, H.G. 1908. Notes on Some Species of Notodontidae in the Collection of the United States National Museum, with Descriptions of New Genera and Species. Proc. Entom. Soc. Wash. 9:45-69.

——— 1924. New Lepidoptera from Mexico and One from Argentina. Insec. Ins. Mens. 12:15-17.

EBERHARD, W.G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Massachussetts.

FELDER, R. 1874. Lepidoptera. Pages 537-548, plates 75-120, in, Reise der oesterreichischen Fregatte Novara. Heft IV. Atlas der Heterocera, Sphingida -Noctuida (C. Felder, R. Felder, R. and A.F. Rogenhofer, authors).

FERGUSON, D.C. 1985. Contributions Toward Reclassification of the World Genera of the Tribe Arctiini, Part 1 - Introduction and a Revision of the *Neoarctia - Grammia* Group (Lepidoptera: Arctiidae: Arctiinae). Entomography 3:181-275.

FORBES, W.T.M. 1916. On the Tympanum of Certain Lepidoptera. Psyche 23:183-192.

——— 1923. Lepidoptera of New York and Neighboring States. Primitive forms. Microlepidoptera. Pyraloids. Bombyces. Agric. Exp. Sta., Cornell Univ.,

Ithaca, New York. Memoir 68 [reprinted 1969 by Entomological Reprint Specialists.]

—— 1939a. The Lepidoptera of Barro Colorado Island, Panama. Notodontidae. Bull. Mus. Comp. Zool. Harvard 85:234-321.

—— 1939b. The Muscles of the Lepidopterous Male Genitalia. Ann. Entom. Soc. Amer. 32:1-10.

—— 1948. Lepidoptera of New York and Neighboring States. Part II. Geometridae. Sphingidae. Notodontidae. Lymantriidae. Agric. Exp. Sta., Cornell Univ., Ithaca, New York. Memoir 274.

—— 1954. Lepidoptera of New York and Neighboring States. Part III. Noctuidae. Agric. Exp. Sta. Cornell Univ. Ithaca, New York. Memoir 274.

Franclemont, J.G. 1946. A revision of the species of *Symmerista* Huebner known to occur north of the Mexican border (Lepidoptera, Notodontidae). Can. Entomol. 78:96-103.

—— 1948. *Symmerista*. pp. 222-224 in Lepidoptera of New York and Neighboring States. Part II. Geometridae. Sphingidae. Notodontidae. Lymantriidae. Agric. Exp. Sta. Cornell Univ. Ithaca, New York. Memoir 274.

FULLARD, J.H. 1984. External Auditory Structures in Two Species of Neotropical Notodontid Moths. J. Comp. Physiol.(Series A) 155:625-632.

GODFREY, G.L. & J.E. APPLEBY. 1987. Notodontidae (Noctuoidea). in F.W. Stehr ed. Immature insects Kendall-Hunt, Dubuque, Iowa.

GROTE, A.M. 1895. List of North American Eupterotidae, Ptilodontidae, Thyatiridae, Apatelidae and Agrotidae. Abhand. heraus. naturwiss. Ver. zu Bremen, 14:1-11.

GUENÉE, M. A. 1852. Noctuélites, Tome II. in M. Boiduval and M. A. Guenée, eds. Historie naturelle des insectes: species général des Lépidoptères, vol. 6: 444 pp. Paris: Librairie Encyclopedique de Roret.

HERRICH-SCHÄFFER, G.A.W. 1855 [1850-1858]. Sammlungem neuer oder wenig bekannter aussereur. Schmetterlinges, I. Regenberg, G.J. Manz. 84 pages, 551 figures on unnumbered plates.

HEPPNER, J.B. & G. LAMAS. 1982. Acronyms for World Museum Collections of Insects, with an Emphasis on Neotropical Lepidoptera. Bull. Entom. Soc. Amer. 28:305-315.

HERING, E.M. 1925. Dioptidae. pp. 501-534 in A. Seitz ed./ Die Gross-Schmetterlinge der Erde. Die Gross-Schmetterlinge des Amerikanischen Faunengebeites. Vol. 6. Die Amerikanischen Spinner und Schwaemer. Alfred Kernen, Stuttgart.

HOLLOWAY, J.D. 1983. The Moths of Borneo. Part 4. Notodontidae. Malay. Nat. J. 37:1-107.

HOLLOWAY, J.D., J.D. BRADLEY & J.D. CARTER. 1987. Lepidoptera. in Betts ed./CIE Guides to Insects of Importance to Man Vol. 1, Wallingford, CAB International.

HÜBNER, J. 1819. Verzeichniss bekannter Schmetterling, verfasst von Jacob Hübner. Ausburg, Verfasser.

—— 1821. Verzeichniss bekannter Schmetterling, verfasst von Jacob Hübner. Ausburg, Verfasser.

JANSE, A.J.T. 1920. On the South African Notodontidae with Descriptions of apparently New Genera and Species. Ann. Transvaal Mus. Pretoria 7:121-124.

JORDAN, K. 1923. On the Comb Bearing Flap Present on the Fourth Abdominal Segment in the Males of Certain Notodontidae. Novit. Zool. 30:153-154.

KIRBY, W.F. 1892. A Synonymic Catalogue of Lepidoptera Heterocera. (Moths) Volume 1. Sphinges and Bombyces. Gurney and Jackson, London, 952 pages.

KIRIAKOFF, S.G. 1950a. Reserches sur les Organes Tympaniques des Lépidoptères en Rapport avec la Classification. III. Dioptidae. Annal. Soc. Entomol. Belgique 86:67-86.

KIRIAKOFF, S.G. 1950b. Sur la Classification et la Phylogénie de la Superfamille Notodontoidea. Annal. Soc. Entomol. Belgique 86:236-235.

—— 1950c. Reserches sur les Organes Tympaniques des Lépidoptères en Rapport avec la Classification. IV. Notodontidae. Biol. Jaarbboek (Dodonaea) 17:66-111.

—— 1970. Lepidoptera Fam. Thaumetopoeidae. Genera Insectorum 219:1-54.

—— 1981. New and known Notodontidae from East and South Africa (Lepidoptera, Notodontoidea). Entomofauna 2:11-31.

KLOTS, A.B. 1970. Lepidoptera. pp. 115-130, in S. L. Tuxen, ed./ Taxonomist's Glossary of Genitalia in Insects, second edition. Munksgaard, Copenhagen.

KRISTENSEN, N.P. 1984. Studies on the Morphology and Systematics of Primitive Lepidoptera (Insecta). Steenstrupia 10:141-191.

LINNAEUS, C. 1758. Caroli Linnaei Systema naturae. Photographic facsimile of the first volume of the 10th edition (1758) Regnum animale. London, Brit. Mus. (Nat. Hist.), facsimile published 1939.

MARUMO, N. 1920. A revision of the Notodontidae of Japan, Corea and Formosa with descriptions of five new genera and five new species. J. Coll. Agric. Imp. Univ. Tokyo 4:273-359.

McCOLL, H.P. 1969. The Sexual Scent Organs of Male Lepidoptera. Masters Thesis. Swansea University College, Wales.

MILLER, J.S. 1987. Revision of the Genus *Phryganidia* Packard, with Description of a New Species (Lepidoptera: Dioptidae). Proc. Entom. Soc. Wash. 89:303-321.

—— 1988. External Genitalic Morphology and Copulatory Mechanism of *Cyanotrichia necyria* (Felder) (Dioptidae). J. Lepid. Soc. 42:103-115.

—— 1991. Cladistics and Classification of the Notodontidae (Lepidoptera: Noctuoidea) based on Larval and Adult Morphology. Bull. Amer. Mus. Nat. Hist. 204:1-230.

—— 1992. Host-Plant Associations among Prominent Moths. BioScience 42:50-57.

MILLER, J.S. & L.D. OTERO. 1994. Immature stages of Venezuelan Dioptinae (Notodontidae in Josia and *Thirmida*. J. Lepid. Soc. 48:388-392.

MINET, J. 1983. Eléments sur la systematique des Notodontidae et nouvelles données concernant leur étude faunistique a Madagascar (Lepidoptera: Noctuoidea. Bull. Soc. Entomol. France 87:354-370.

MOSCHLER, H.B. 1878. Beiträge zur Schmetterlings -Fauna von Surinam. II. Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien, 27:629-700, pls 8-10.

—— 1883. Beiträge zur Schmetterlings - Fauna von Surinam. V. Supplement. Verhandl. Zool.-bot. Gesell. Wien, 32:303-362. pls 7,8.

—— 1886. Beiträge zur Schmetterlings - Fauna von Jamaica. Abhandl. heraus. Seckenberg natur. Gesell. (Frankfort), 14:25-84.

OSETO, C.Y. & T.J. HELMS. 1976. Anatomy of the Adults of *Loxagrotis albicosta* Hbn. Univ. Nebraska Studies, New Series No. 52.

PACKARD, A.S. 1864. Synopsis of the Bombycidae of the United States. Part II. Proc. Entom. Soc. Philadelphia, 3:331-396.

—— 1895. Monograph of the Bombycine Moths of America North of Mexico including their Transformations and Origin of the Larval Markings and Armature, Part 1: family 1, Notodontidae. Mem. Nat. Acad. Science 7:7-287.

PIERCE, F.N. 1914. The Genitalia of the Group Geometridae of the Lepidoptera of the British Islands. Liverpool.

RICHARDS, A.G. 1932. Comparative Skeletal Morphology of the Noctuid Tympanum. Entomologica Amer. 13:1-43.

SCHAUS, W. 1901. Revision of the American Family Notodontidae. Trans. Entom. Soc., London 1901:257-343.

SIBATANI, A. 1972. Male Genitalia of Lepidoptera: Morphology and Nomenclature IV. Notes on Tuxen's "Taxonomist's Glossary of Genitalia in Insects": Second enlarged edition. J. Lepid. Soc. 26:117-112.

SIBATANI, A., M. OGATA, Y. IKADA & H. OKAGAKI. 1954. Male Genitalia: Morphology and Nomenclature. I. Divisions of the Valvae in Rhopalocera, Phalaenidae (Noctuidae) and Geometridae. Ann. Entom. Soc. Amer. 47:93-106.

SICK, H. 1940. Beitrag zur Kenntnis der Dioptidae, Notodontidae und Thaumetopoeidae und deren Verwandtschaftsbeziehungen zueinander. Zool. Jahrb. (Anat.) 66:263-290.

STEKOLNIKOV, A.A. 1967. Functional Morphology of the Copulatory Apparatus in the Primitive Lepidoptera and General Evolutionary Trends in the Genitalia of the Lepidoptera. Entom. Rev. 46:400-409.

STEKOLNIKOV, A.A. & V.I. KUZNETSOV. 1986. Origin and General Direction of Evolution of the Skeleton and Musculature of the Male Genitalia in Lepidoptera. Entom. Rev. 65:130-145.

SURLYKKE, A. 1984. Hearing in Notodontid Moths: a Tympanic Organ with a Single Auditory Neurone. J. Exp. Biol. 113:323-335.

THIAUCOURT, P. 1975. Une Nouvelle Espece de *Dasylophia* du Yucatan (Lep. Notodontidae). Lambillionea LXXV:89-91.

—— 1980. Deux Nouveaux *Marthula* Walker (Lep. Notodontidae). Lambillionea LXXIX:84-87.

—— 1985. Deux Nouvelles Especes de *Calledema* Butler (Lepidoptera, Notodontidae). Nouv. Rev. Entom. 4:371-375.

—— 1987. Notodontidae Nouveaux de Guyane française (Lepidop. Heterocera). Lambillionea LXXXVII (5-6):50-61.

TIKHOMIROV, A. M. 1979. The Functional Morphology of the Male Genital Apparatus and Taxonomic Division of the European Notodontidae (Lepidoptera). Trudy Zool. Inst. Lenin. 83:104-119.

WALKER, F. 1855. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 5:977-1257. Edward Newman, London.

—— 1856. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 9:1-252. Edward Newman, London.

—— 1857. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 11:493-764. Edward Newman, London.

—— 1858a. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 13:983-1236. Edward Newman, London.

—— 1858b. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 14:1237-1519. Edward Newman, London.

—— 1858c. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. 15:1521-1888. Edward Newman, London.

—— 1862. Characters of Undescribed Lepidoptera in the Collection of W.W. Saunders, Esp. Trans. Entom. Soc. London, series 3, 1:70-128.

—— 1865. List of the Specimens Lepidopterous insects in the Collection of the British Museum. Volume 33, Supplement Part 3. Edward Newman, London. pages 707-1120.

—— 1869. Characters of Uundescribed Lepidoptera Heterocera. E.W. Janson, London, 112 pages.

WELLER, S.J. 1989. *Phylogeny of the Nystaleini* (Lepidoptera: Noctuoidea: Notodontidae). Ph.D. Dissertation, University of Texas at Austin. Univ. Microfilms Inc., Ann Arbor, MI, microfilm order #8920869.

—— 1990. Revision of the *Nystalea aequipars* Species-Complex. J. New York Entom. Soc. 98:35-49.

—— 1991. Revision of the *Pentobesa xylinoides* (Walker) Species Group (Lepidoptera: Notodontidae). Proc. Entom. Soc. Wash. 93:795-807.

# A Reconsideration of the Taxonomic Status of *Euphydryas editha koreti* (Lepidoptera: Nymphalidae) from the Central Great Basin

Hugh B. Britten[1], Peter F. Brussard[1], and Dennis D. Murphy[2]

[1] Biological Resources Research Center, Department of Biology, University of Nevada, Reno, NV 89557
[2] Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305

**Abstract.** Samples of *Euphydryas editha lehmani* and *Euphydryas editha koreti* from the central Great Basin and *Euphydryas editha gunnisonensis* from the western and central Rocky Mountains of Utah and Colorado were assayed for isozyme variability at 19 protein loci. Genetic identity estimates and the resulting phenogram show that *Euphydryas editha koreti* is not genetically differentiated from *Euphydryas editha lehmani*. These results are consistent with the spatial distribution of *Euphydryas editha koreti* which exists as a number of isolated alpine populations. They also suggest that Koret's checkerspot butterfly is not a cohesive evolutionarily significant unit and thus may not warrant subspecific status.

## INTRODUCTION

Koret's checkerspot butterfly, *Euphydryas editha koreti* (Murphy and Ehrlich 1983), was described from high alpine ridges and slopes on isolated mountain ranges in the Great Basin. The subspecies is distinguished from a more widespread Great Basin subspecies, *Euphydryas editha lehmani* (Gunder 1929), by its much smaller size and greater yellow coloration of the submarginal band on its dorsal hindwing (Murphy and Ehrlich 1983, Austin and Murphy 1995).

In addition to that quite consistent morphological distinctiveness, *Euphydryas editha koreti* was acknowledged with subspecific status because of several marked ecological differences with *Euphydryas editha lehmani* (Murphy and Ehrlich 1983). Dramatic elevational differences exist between the habitats of the two subspecies; *Euphydryas editha lehmani* occurs from 1600 m to 2500 m in elevation, while *Euphydryas editha koreti* occurs above 3700 m. *Euphydryas editha koreti* apparently oviposits exclusively on *Castilleja lapidicola*, while *Euphydryas editha lehmani* oviposits on *C. chromosa* and *Pedicularis semibarbata* across most of its Great Basin distribution, and on *C. linariifolia* in the Pequop Mountains (Murphy and Ehrlich 1983). Finally, *Euphydryas editha lehmani* tends to fly in late May or early June, while the flight season for *Euphydryas editha koreti* is often delayed until early July, or in some years, late July. Individuals

assignable to the two subspecies have never been observed flying together.

These phenotypic and ecological differences notwithstanding, substantial doubt is cast on the appropriateness of designating populations currently assigned to *Euphydryas editha koreti* as a subspecies distinct from *Euphydryas editha lehmani*. Here, we present allozyme data that indicate that *Euphydryas editha koreti* is not particularly well differentiated genetically from *Euphydryas editha lehmani* and that populations of Koret's checkerspot butterfly do not constitute a coherent evolutionary entity with common immediate ancestry.

## MATERIALS AND METHODS

Specimens of *Euphydryas editha lehmani* were collected from a total of seven localities in seven Great Basin mountain ranges (Toiyabe Range, Toquima Range, Monitor Range, White Pine Mountains, Egan Range, Schell Creek Range, and Snake Range), and *Euphydryas editha koreti* was collected from three localities; one each in the Toiyabe, Schell Creek, and the Snake Ranges (Figure 1). In addition, seven samples of *Euphydryas editha gunnisonensis* were collected from the Rocky Mountains of Utah and Colorado (Britten et al. 1994). This sampling regime provided the opportunity to compare genetic differences among the three *Euphydryas* subspecies, with the two subspecies from the Great Basin being represented by isolated but interspersed populations, and the Rocky Mountain subspecies being geographically separate from the other two (Figure 1). All samples were collected between 1980 and 1983.

Allozyme variation was assayed at 19 presumptive loci using horizontal starch-gel electrophoresis. Details of allozyme assay methods can be found in Brussard et al. (1985) and Baughman et al. (1990).

Nei's (1978) unbiased genetic identities were calculated between each pair of samples in the study. This index of genetic similarity based on allele frequencies provides a metric that can be used to derive a phenogram that is a graphical representation of the genetic similarities among the assayed populations. The UPGMA clustering algorithm was used in this analysis. BIOSYS-1 (Swofford and Selander 1981) was used for all data analyses.

## RESULTS

Total sample sizes were 143 for *Euphydryas editha koreti*, 282 for *Euphydryas editha lehmani*, and 438 for *Euphydryas editha gunnisonensis*. Unbiased genetic identities (Nei 1978) among the 17 *Euphydryas editha* populations sampled are given in Table 1. Mean observed population heterozygosities were nearly identical among the three subspecies; $0.057 \pm 0.009$, $0.058 \pm 0.022$, and $0.061 \pm 0.023$ for *Euphydryas editha koreti*, *Euphydryas editha lehmani*, and *Euphydryas editha gunnisonensis*, respectively. Genetic identities of 1.00 were estimated among three of the four Gunnison Basin populations (AL, AS, and JC) and between NS, an *Euphydryas editha koreti* sample from the Schell Creek Range, and ANT, an *Euphydryas editha lehmani*
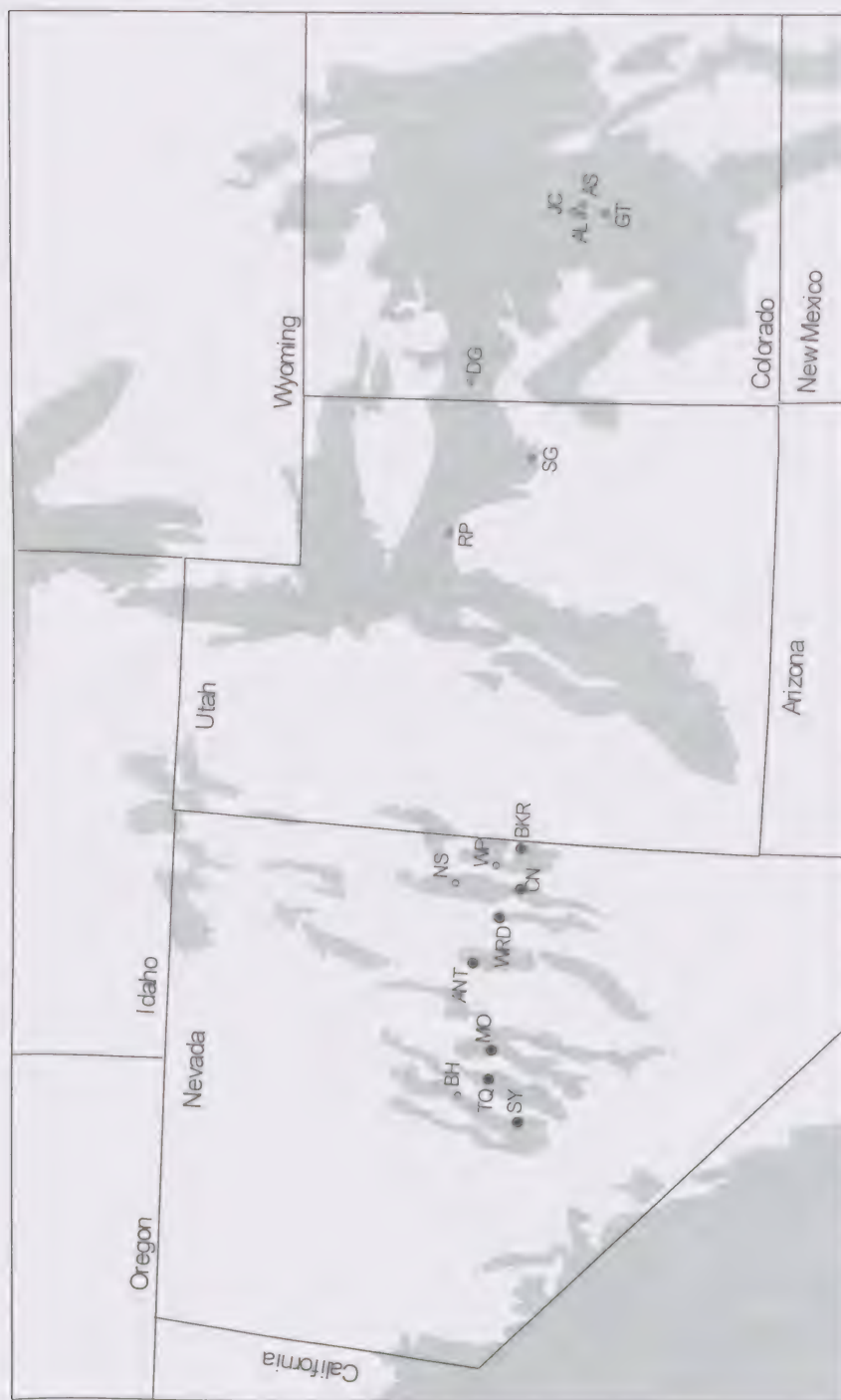
Figure 1. Map of *Euphydryas editha* collection sites with subspecies *Euphydryas editha koreti* (open circles), *Euphydryas editha lehmani* (closed circles), and *Euphydryas editha gunnisonensis* (dotted circles) indicated. Shading represents areas over 2,200 meters elevation.

Table 1. Pairwise estimates of unbiased genetic identity (Nei 1978) for 17 samples of *Euphydryas editha*. Subspecies *lehmani* and *koreti* were sampled from Nevada and subspecies *gunnisonensis* was sampled from Utah and Colorado.

| Population | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 SY *lehmani* | ***** | | | | | | | | | | | | | | | |
| 2 BH *koreti* | 0.994 | | | | | | | | | | | | | | | |
| 3 TQ *lehmani* | 0.983 | 0.984 | | | | | | | | | | | | | | |
| 4 MO *lehmani* | 0.992 | 0.993 | 0.993 | | | | | | | | | | | | | |
| 5 ANT *lehmani* | 0.992 | 0.992 | 0.991 | 0.997 | | | | | | | | | | | | |
| 6 WRD *lehmani* | 0.994 | 0.993 | 0.995 | 0.999 | 0.997 | | | | | | | | | | | |
| 7 NS *koreti* | 0.993 | 0.991 | 0.994 | 0.998 | 1.000 | 0.999 | | | | | | | | | | |
| 8 CN *lehmani* | 0.991 | 0.991 | 0.997 | 0.998 | 0.996 | 0.999 | 0.998 | | | | | | | | | |
| 9 WP *koreti* | 0.986 | 0.987 | 0.993 | 0.996 | 0.999 | 0.995 | 0.998 | 0.995 | | | | | | | | |
| 10 BKR *lehmani* | 0.987 | 0.986 | 0.986 | 0.993 | 0.996 | 0.992 | 0.996 | 0.991 | 0.996 | | | | | | | |
| 11 RP *gunnisonensis* | 0.951 | 0.947 | 0.956 | 0.960 | 0.973 | 0.959 | 0.970 | 0.958 | 0.978 | 0.977 | | | | | | |
| 12 SG *gunnisonensis* | 0.962 | 0.958 | 0.968 | 0.969 | 0.982 | 0.969 | 0.979 | 0.968 | 0.987 | 0.983 | 0.996 | | | | | |
| 13 DG *gunnisonensis* | 0.956 | 0.955 | 0.963 | 0.964 | 0.979 | 0.963 | 0.974 | 0.963 | 0.983 | 0.979 | 0.994 | 0.998 | | | | |
| 14 GT *gunnisonensis* | 0.967 | 0.967 | 0.973 | 0.976 | 0.987 | 0.975 | 0.983 | 0.973 | 0.990 | 0.986 | 0.990 | 0.995 | 0.997 | | | |
| 15 AS *gunnisonensis* | 0.947 | 0.947 | 0.957 | 0.959 | 0.974 | 0.956 | 0.968 | 0.956 | 0.979 | 0.975 | 0.992 | 0.996 | 0.999 | 0.997 | | |
| 16 JC *gunnisonensis* | 0.957 | 0.957 | 0.966 | 0.969 | 0.982 | 0.967 | 0.976 | 0.966 | 0.986 | 0.982 | 0.993 | 0.997 | 0.999 | 0.999 | 1.000 | |
| 17 AL *gunnisonensis* | 0.955 | 0.954 | 0.963 | 0.965 | 0.979 | 0.963 | 0.974 | 0.962 | 0.983 | 0.980 | 0.994 | 0.997 | 0.999 | 0.999 | 1.000 | 1.000 |

sample from the White Pine Mountains (Table 1). The lowest estimates of genetic identity (I=0.95) were found between *Euphydryas editha gunnisonensis* populations from the central Rocky Mountains and *Euphydryas editha lehmani* and *Euphydryas editha koreti* samples from the Toiyabe Range. The UPGMA phenogram derived from genetic identity estimates separates *Euphydryas editha gunnisonensis* from the other two subspecies included in the study, while *Euphydryas editha koreti* samples are imbedded among *Euphydryas editha lehmani* samples (Figure 2). *Euphydryas editha gunnisonensis* is separated from the other subspecies at a mean genetic identity of about 0.97 (Figure 2).

## DISCUSSION

Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." It has long been recognized, therefore, that the subspecies category does not necessarily reflect patterns of differentiation that have evolutionary significance; hence the category should be used only to delineate groupings of populations that share phenotypic similarity (Wilson and Brown 1953). Debate has continued since the 1950's over the taxonomic importance of the subspecies category and how the category should be defined (Ehrlich 1957, Lidicker 1962, Mayr 1982, Cracraft 1989). The purpose here is not to revisit that debate, but to point to the general agreement that the possession of a trinomial appellation by a group of populations does not necessarily mean that those populations constitute an evolutionarily significant unit (Mayr 1982, Cracraft 1989). The subspecies category should be used simply as a convenience for delineating groups of geographically proximate, morphologically similar forms discernable from other such groups (Mayr 1982). In that light, the interspersed distribution of *Euphydryas editha lehmani* and *Euphydryas editha koreti* presents a taxonomic problem.

The suite of alpine populations of *Euphydryas editha* found in the Schell Creek, Snake, and Toiyabe Ranges of Nevada was described as the subspecies *Euphydryas editha koreti* Murphy and Ehrlich based on ecological and morphological differences of these individuals when compared to specimens of the more widespread montane subspecies found at lower elevations, *Euphydryas editha lehmani*. Although all *Euphydryas editha koreti* populations are found in nearly identical ecological situations, they are completely isolated from one another and are at least partially surrounded by *Euphydryas editha lehmani* populations at lower elevations (Figure 1). Because of those discontinuities in the distribution of *Euphydryas editha koreti* (Figure 1), this subspecies is described as "polytopic," that is, it shows "independent recurrence of similar or phenotypically indistinguishable populations in geographically separated areas" (Mayr 1969). For many workers this current
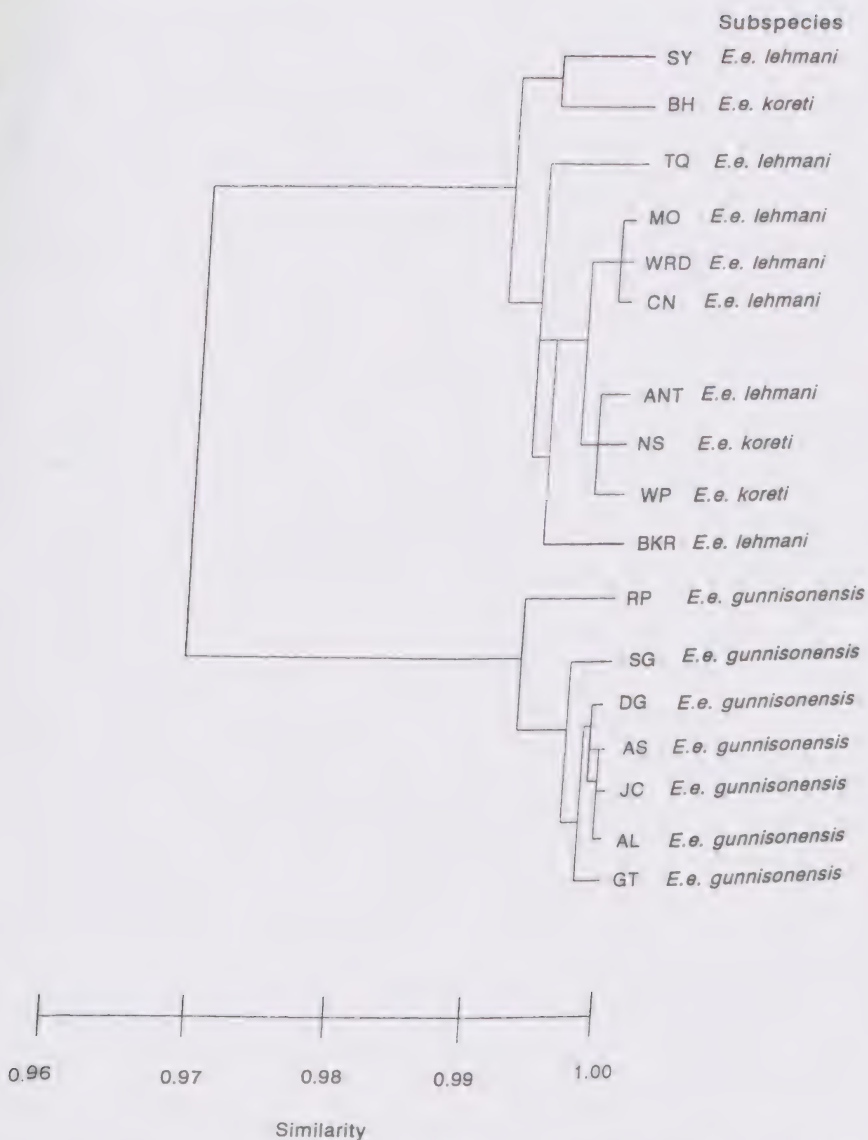
Figure 2. UPGMA phenogram based on Nei's (1978) unbiased genetic identities for 17 sampled populations of *Euphydryas editha*. Three subspecies are represented: *Euphydryas editha lehmani* and *Euphydryas editha koreti* from Nevada, and *Euphydryas editha gunnisonensis* from Utah and Colorado. Cophenetic correlation coefficient is 0.885. Note that the relationships involving the BKR and AS populations are incompletely resolved on the phenogram.

spatial distribution, this polytopy, disqualifies *Euphydryas editha koreti* from subspecies status (e.g. Wilson and Brown 1953, Mayr 1963 and 1969). If, however, populations referred to as *Euphydryas editha koreti* were to show high levels of genetic similarity to one another when compared to geographically adjacent populations of the same species, common ancestry could be inferred for *Euphydryas editha koreti* populations. This would suggest a more continuous distribution in the past, and perhaps defensible subspecific status.

The allozyme results presented do not show such coherence, and they provide little support for the subspecific status of *Euphydryas editha koreti*. This conclusion is based on the UPGMA phenogram in Figure 2 and the geographic distribution of *Euphydryas editha koreti*. Previous work by Brussard et al. (1985), using nearly identical methods, provided a framework from which taxonomic decisions can be made using allozyme data at taxonomic levels below the subfamily. The mean genetic identity among 12 subspecies in the tribe Melitaeini, including several *Euphydryas editha* subspecies, was 0.964 (Brussard et al. 1985). This estimate of mean identity is nearly equal to the genetic identity observed between the *Euphydryas editha gunnisonensis* and *Euphydryas editha lehmani - Euphydryas editha koreti* clusters in Figure 2. This result suggests that at least some "good" subspecies exist among montane *Euphydryas editha* populations in the central Great Basin and Rocky Mountain regions.

The clustering of *Euphydryas editha koreti* with *Euphydryas editha lehmani*, however, indicates much greater genetic similarity among these populations and supports the conclusion that *Euphydryas editha koreti* is probably not an evolutionarily significant unit, but is instead a recurrent high elevation phenotype of *Euphydryas editha lehmani*. While it is impossible to dismiss a scenario in which low elevation populations were established from ancestral high elevation populations, and subsequently became the most widespread phenotype in the Great Basin; the most likely biogeographic scenario is that different low elevation populations have given rise independently to alpine populations sharing convergent phenotypes in the three Great Basin mountain ranges where *Euphydryas editha koreti* is known to occur. The tight clustering of the Toiyabe Range samples, one of *Euphydryas editha lehmani* (SY, Figure 1) and the other *Euphydryas editha koreti* (BH, Figure 1), in the phenogram (Figure 2) provides the best evidence of a high degree of similarity between these two taxa. The allozyme data suggest that, despite the phenotypic similarity of individuals from populations assigned to *Euphydryas editha koreti* and their distinctiveness from individuals from geographically adjacent areas, they should not be recognized as taxonomically distinct from the more widespread *Euphydryas editha lehmani*. Furthermore, the data also suggest that *Euphydryas editha koreti* are not evolutionarily distinct from nearby *Euphydryas editha lehmani* populations at lower elevations.

The *Euphydryas editha koreti* situation underscores the lack of formal nomenclatural tools available to describe phenotypically distinct entities that do not fit the subspecies category. This difficulty is expected to be particularly acute for well studied taxa, such as Lepidoptera, for which there is a long standing tradition of "splitting." Current nomenclatural precedence would call for the "sinking" of *Euphydryas editha koreti* into the subspecies *Euphydryas editha lehmani*. This approach, however, would leave a morphologically distinct form, now referred to as *Euphydryas editha koreti*, without the unique designation. Another approach would be to recognize an additional taxonomic category for polytopic subspecies. This approach is neither particularly parsimonious nor traditional, is likely to be cumbersome, and its application would surely meet resistance. It is clear that this sort of taxonomic dilemma will only increase in frequency as molecular genetic techniques become more widely available and the taxonomic status of an increasingly broad spectrum of organisms comes under scrutiny.

## LITERATURE CITED

AUSTIN, G.T. & D.D. MURPHY. 1995. *Euphydryas editha* of the Great Basin with descriptions of three new subspecies. pp. 407-418. In T.C. Emmel, et al., eds. Systematics of western North American butterflies. In press.

BAUGHMAN, J.F., P.F. BRUSSARD, P.R. EHRLICH & D.D. MURPHY. 1990. History, selection, drift, & gene flow: Complex differentiation in checkerspot butterflies. Canadian Journal of Zoology 68: 1967-1975.

BRITTEN, H.B., P.F.BRUSSARD, D.D. MURPHY & P.R. EHRLICH. 1995. A test for isolation-by-distance in central Rocky Mountain and Great Basin *Euphydryas editha* populations. Journal of Heredity (86: 204-210).

BRUSSARD, P.F., P.R. EHRLICH, D.D. MURPHY, B.A. WILCOX & J. WRIGHT. 1985. Genetic distances and the taxonomy of checkerspot butterflies (Nymphalidae: Nymphalinae). Journal of the Kansas Entomological Society 58: 403-412.

CRACRAFT, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pages 28-59 In D. Otte & Endler, J.A., eds. Speciation and its consequences. Sinauer Associates, Inc., Sunderland, MA.

EHRLICH, P.R. 1957. Systematists and subspecies. The Lepidopterists' News 11: 155-157.

LIDICKER, W. Z., Jr. 1962. The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology 11: 160-171.

MAYR, E. 1963. Animal species and evolution. The Belknap Press, Cambridge, MA. 797 pages.

——. 1969. Principles of systematic zoology. McGraw-Hill Book Company, New York. 428 pages.

——. 1982. The growth of biological thought: Diversity, evolution, and inheritance. The Belknap Press, Cambridge, MA. 974 Pages.

MURPHY, D.D. & P.R. EHRLICH. 1983. Biosystematics of the *Euphydryas* of the central Great Basin with the description of a new subspecies. Journal of Research on the Lepidoptera 22: 254-261.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

SWOFFORD, D.L. & R. B. SELANDER. 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and evolution. Journal of Heredity 72: 281-283.

WILSON, E.O. & W.L. BROWN. 1953. The subspecies concept and its taxonomic application. Systematic Zoology 2: 97-111.

## Notes

### A report on the reproductive morphology of gynander tasar silkmoths *Antheraea mylitta* Drury (Lepidoptera: Saturniidae)

Gynandromorphs are abnormal individuals showing varying degrees of mixed sexual characters. They are known for several insect groups, but are most often encountered in Lepidoptera (Scriber and Evans 1987, Davies 1988, Halstead 1989, Blackaller-Bages and Delgado-Castillo 1990, Forattini *et al.* 1991). Gynandromorphs may occur through the failure of genetic sex determining mechanisms or through hormonal or other influences during development. In the extreme case, one half of such an insect is female, the other half male. Some of the tissues are genetically and structurally female, others male. The genetic basis of gynandromorphism in *Drosophila, Lymantria, Bombyx,* etc. is well documented (Sinnott *et al.* 1958; Altenburg, 1970; Herskowitz, 1977). It has been recently established in mites that gynandromorphism is the result of unequal distribution of sex linked chromosomes rather than control at the gene or physiological level (Homsher and Yunker, 1981).

The occurrence of gynandromorphs is very rare in both wild and commercial populations of the tropical tasar silkmoth, *Antheraea mylitta.* Gynandromorphism in this moth was first reported by Sen and Jolly (1967) wherein they discussed the morphological characters with special reference to the genitalia. This note illustrates the previously unreported morphology of the reproductive system of gynander tasar silkmoths.

Two types of gynandromorph were observed in a commercial laboratory population of the tasar silkmoth: predominately male gynandromorphs and predominately female gynandromorphs. In both cases, the left half of the body was observed to possess the male characters whereas the female characters occurred on the right. The male predominants have well developed testes with a male accessory gland on the left half and on the right half a single atrophied ovary with a mature colleterial gland and a female accessory gland (Fig. 1). In the case of female predominants, the reproductive organ situation was reversed. A single ovary containing four mature ovarioles with a single fully developed colleterial gland and female accessory gland was present. In these individuals the testes remained atrophied and non-functional. The female predominant condition is illustrated in Fig. 2. In both male and female predominant individuals, the genitalia retain important parts of both the female (bursa copulatrix) and male (aedeagus).

It is noteworthy that predominant female gynandromorphs, after mating with normal males, laid very few eggs and these were infertile. By contrast, virgin normal females, when mated with predominant male gynandromorphs laid fertile eggs. A similar reproductive behavior has been reported in gynandromorph *Drosophila melanogaster* by Napolitano and Tompkins (1989). Conventional morphological secondary sex characters such as wing maculation and antenna structure show the typical male features on the left and female features on the right side of the body. The physiological and genetic bases of gynandromorphism in tasar silkmoth remain unknown.
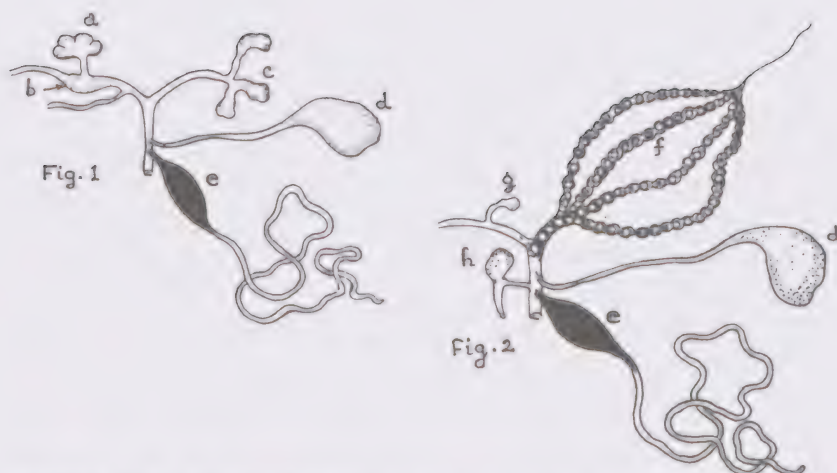
Figures 1 and 2. Reproductive system of predominant male gynandromorph (Fig. 1) and female gynandromorph (Fig. 2) internal reproductive system of *Antheraea mylitta* Drury. Legends: a) mature testis, b) male accessory gland, c) atrophied ovary, d) female accessory gland, e) colleterial gland, f) mature ovary, g) atrophied testis, h) bursa copulatrix.

*Anathbandhu Chaudhuri, Dipankar Chakraborty, and Asok Kumar Sinha. Central Tasar Research and Training Institute, Nagri, Ranchi 835 303, India*

LITERATURE CITED

Altenburg, E. 1970. *Genetics*, Indian Edition, Rinehart and Winston, Inc., New York.

Blackaller-Bages, J. & L. Delgado-Castillo. 1990. A case of gynandromorphy in *Megasoma elephas occidentalia* Bolivar, Jimenez and Martinez (Coleoptera: Melolonthidae). Coleoptera Bull. 44(3): 372-373.

Davies, D. M. 1988. Gynandromorphs in Canadian Simuliidae (Diptera). Proc. Entomol. Soc. Ont. 119: 87-89.

Forattini, O. P., M. A. M. Sallum & D. C. Flores. 1991. Gynandromorphs of some *Culex* (*Melanoconion*) species. Jr. Am. Mosq. Control Assoc. 7(1): 129-131.

Halstead, J. A. 1989. A Gynandromorph of *Hockeria rubra* (Ashmead) (Hymenoptera: Chalcididae). Proc. Entomol. Soc. Wash: 90 (2): 258-259.

Herskowitz, I. H. 1977. Principles of Genetics, 2nd Ed., Macmillan, New York.

Homsher, P. J. & C. E. Yunker. 1981. Bilateral gynandromorphism in *Dermacentor andersoni* (Acari: Ixodidae) morphologic and cytogenetic analysis. Jr. Med. Entomol. 18 (1): 89-91.

Napolitano, L. M. & L. Tompkins. 1989. Neural control of homosexual courtship in *Drosophila melanogaster* . Jr. Neurogenetics 6 (2): 87-94.

Scriber, J. M. & M. H. Evans. 1987. Bilateral gynandromorphs, sexual and/ or color mosaics in the tiger swallowtail butterfly *Papilio glaucus* (Lepidoptera:Papilionidae). Jr. Res. Lepid. 26 (1-4): 39-57.

Sen, S. K. & M. S. Jolly. 1967. Occurrence of gynandromorphism in tasar silkmoth (*Antheraea mylitta* Drury). Curr. Sci. 36 (14): 385-386.

Sinnott, E. W., L. C. Dunn & T. Dobzhansky. 1958. Principles of Genetics, 5th Ed., McGraw-Hill, New York.

## Notes on the Santa Monica Mountains hairstreak *Satyrium auretorum fumosum* Emmel and Mattoni

Since naming this subspecies (Emmel, J. and R. Mattoni. 1990. Jr. Res. Lepid. 28:105-111) several new observations have been made that bear on its conservation biology. Although the life history remains to be formally described, one rearing cycle has been observed in captivity by J. Emmel from eggs laid by a captive female taken 16 June 90 on *Eriogonum fasciculatum* at Carlisle Canyon, Los Angeles Co., CA . The female producing these eggs was confined by Pasko with scrub oak, *Quercus berberidifolia*, but the c. 25 ova recovered were all found embedded in the depressions of the paper toweling lining the bottom of the box. Egg diapause was followed by 15 larvae emerging in late spring with all larvae feeding to pupation and eclosion. The 10 larvae retained by Pasko were reluctant to start feeding on the fresh but mature shoots of *Q. berberidifolia* provided for food. The earlier hypothesis of Emmel and Mattoni asserted that the butterfly was restricted to scrub oaks, mostly *Q. berberidifolia* in the Santa Monica Mountains, a relative of the known scrub oak foodplant of the nominate subspecies. Adults were never observed on or around scrub oak in the Santa Monica Mountains. Until now *fumosum* appeared to have a highly limited distribution and was also very sparse where found. This represents an unusual pattern for an insect taxon unless it were near a terminal stage of extinction.

Initial field observations noted that adults were rarely found nectaring, and when nectaring was observed the source was always common buckwheat, *Eriogonum fasciculatum*. On 29 May 1993 Pasko again observed several flight worn *fumosum* nectaring at the small isolated patch of *E. fasciculatum* in Carlisle Canyon where the 1990 specimens were taken. Nearby were two small scrub oaks and several large trees of coast live oak, *Q. agrifolia*. Upon tapping the branches of both oak species, one male *fumosum* was obtained from *Q. agrifolia*. Further searching led to the discovery of several of both sexes on another *Q.agrifolia* several hundred feet away from the first tree. No additional adults were observed from ten other trees in the vicinity. On 23 April 1994 Pasko confirmed *Q. agrifolia* as the correct foodplant by collecting eight last instar larvae in the field at the Carlisle Canyon site. These larvae were taken by beating the lower terminal branches that bore young and tender new growth leaves.

At this Carlisle Canyon site a group of about 25 mature *Q.agrifolia* trees form an isolated patch as an oak savannah association within which *fumosum* larvae were found on only four trees. Many of these trees, however, are large and cannot be adequately sampled for either larvae or adults. Ants were always present, but specimens were not retained for identification and no specific ant-larvae interactions were seen although the species is known to be strongly attractive to ants (G. Ballmer, pers. comm.). Large numbers of microlepidoptera larvae were also present that could account for the presence of the large number of ants.

Five of the eight larvae were parasitized by an unidentified species of small Diptera. The three survivors located pupation sites within two days and eclosed

indoors between 12 and 15 May 1994. Several visits to the Carlisle Canyon site failed to produce sightings of adults until 28 May. In 1993 most adults were flight-worn by this date. On May 28 two adults were found on the same tree that yielded the 1993 females and the 1994 larvae. On 4 June 1994 five additional adults were taken and four more seen, again on the same tree with none on any other tree at the site. The small *Eriogonum* patch was just starting to bloom and no adults were observed.

The following day, with knowledge of foodplant and flight time confirmed, another live oak savannah stand was visited near Lake Malibu (*fumosum* type locality) in the Santa Monica Mountains National Recreation Area . Tapping the lower branches of several live oak trees quickly yielded adult *fumosum*. As at Carlisle Canyon, adults are sedentary and fly up only when disturbed. However, they return to perch within a few seconds, a behavior more pronounced for females. Males were occasionally observed to engage in short chases with one another before settling. A colony of the copper *Tharsalea arota nubila* occurs at this site and many males simultaneously perched on the outer branches of the live oaks. The male coppers, easy to discriminate by their larger size and lighter color than *fumosum,* tended to fly somewhat longer after disturbance. At this site *fumosum* is more abundant that at Carlisle, but by no means common. Butterflies were observed on seven trees out of 20 examined. A number of additional trees were present but not examined because of the hilly terrain and heavy understory.

Several males were observed nectaring in two separate small *E. fasciculatum* patches. A second visit on 11 June resulted in the observation of three males and five females on the oaks and four males nectaring on *Eriogonum*. A final visit on 17 June provided no observations at this site or at any of four other live oak savannah assemblages in the vicinity. No adults were observed on the few scrub oaks in the area. From observations over the past four years, nectaring usually occurs between 1100 and 1330 hours, although on hot days they may be observed nectaring as late as 1600.

Although *Q. agrifolia* is abundant and widespread across the northwest slopes of the Santa Monica Mountains, many trees are on private property or other disturbed land where much of the undergrowth, including *E. fasciculatum,* has been altered or removed. What effect this may have on *fumosum* populations is unclear. The advent of frequent anthropogenic fires in the area is another potential threat since ova diapause on oak branches.

As a further note to adult feeding, Mattoni earlier observed *S. auretorum spadix* near Lebec, CA imbibing on excretions from scale insects found on its scrub oak host at that locality. Several adults were observed simultaneously feeding in this manner on two scale colonies. Adults were rarely seen at floral nectar sources and were generally thought to be scarce.

In summary: 1) Adults of the subspecies *S. auretorum fumosum* spend most of their time perching only on coast live oak trees *Quercus agrifolia*. 2) Populations seem to be restricted to only a few "choice" trees with succulent leaves when a number of trees are available. 3) Individual adults appear highly sedentary. 4) The populations appear structured as a series of metapopulations with minimum interchanges among colonies, each delineated by an individual tree. 5) There is not a uniform population continuous with the live oak savannah of the region. 6) Adults rarely nectar, and when they do they were observed only on *Eriogonum fasciculatum*. Adults may take sustenance from scale insect secretions or possi-

bly sap runs and slime fluxes. 7) Larvae require very young tender shoots for survival.

We thank the National Park Service, Santa Monica Mountains National Recreation Area for their cooperation in permitting this work. We strongly urge the listing of the species as endangered for the reasons cited.

*John Pasko*, *340 Lynn Oaks Court, Thousand Oaks, CA 91320-4759*
*Rudi Mattoni*, *Department of Geography, UCLA, Los Angeles, CA 90095-1524*

## New courtship posture in females of two Chilean butterflies: Rejective or receptive?

Two species of *Hylephila* Billberg inhabit the large lawns of the Chilean air force academies at the "comuna" El Bosque of Santiago. *H. fasciolata* (Blanchard) Gay and *H. signata* (Blanchard) Gay are on the wing from late August to early May in successive broods. Both are common, successfully surviving the blades of the lawn mowers. The males are typical perchers, using the taller grass blades, flowers of *Taraxacum offincinale* (L.) Wibb., *Leontodon taraxacoides* (Vill.) Merat, *Bellis perennis* L. (all Asteraceae), and bare soil as perching sites from which they intercept passing *Colias vautieri*, *Tatochila mercedis* and their congenerics. In mating couples the female carries the male when disturbed (see *H. signata* couple in Figure 1 with male hanging below). The females have a special way of laying their white, hemispherical, smooth eggs: they walk on the grass with their abdomen curved below and forward, searching for the proper oviposition sites with the exploratory tip of the abdomen.

October 27, 1993 was a typical clear, warm, late spring day in Santiago (air temperature about 28 C). At 14:00 hrs, high flight activity was observed over the lawns. In the air, only a few cm above the grass, a male *H. fasciolata* courted a female. The female landed on the ground on the edge of a small opening in the lawn about 3 inches in diameter. The male landed immediately after her and about 1.5 inches behind. He approached the female in small jumps, each time fluttering his wings in what looked like a showy, ritual "dance." It is possible that the fluttering released pheromones from his front wing androconial patches. During the male's courtship, the female was totally passive and did not move, but when the male got closer, the female suddenly began to vibrate both her hind legs in an up-and-down motion, in effect creating an impenetrable barrier. The behavior appeared to be an effective new repulsive posture. The vibration was too fast to detect whether the legs moved together in parallel or in a scissors-like movement. When the male got closer and was only a few mm behind and to her side, the female flew away.

A few days later (November 1, 1993), 150 km to the north, at Pichicuy, on the Pacific coast, at 15:00 hrs, a low courtship flight of the dwarf blue *Pseudolucia benyamini* Balint was observed. The flight was not more than 30 cm over the ground and among the cushion-like food plants *Chorizanthe vaginata* Benth (Polygonaceae). The female landed on a flowering head and started to walk on it with the male following close behind her. Once again I saw the hind legs vibrating in the female, but within about five seconds they copulated. Thus, it is

Fig. 1    Mating *Hylephila signata* (Blanchard) Gay, Santiago, Chile, 1200m, 10 Dec
1993.

unclear to me whether this copulation was achieved in spite of the "rejecting"
movements or whether the vibration is possibly a receptive posture.   More
observations are needed to establish a final conclusion.

Although nothing has been published specifically on Chilean skippers, general
discussions of mating behavior may be found in Scott, J. A., 1986, *The Butterflies
of North America*, Stanford University Press, California, 583 pp.; Shapiro, I. D,
1975, Courtship and mating behavior of the Fiery skipper, *Hylephila phylaeus*
(Hesperiidae), J. Res. Lepid., 14 (3):125-141; and Shapiro, I. D., 1977, Interaction
of population biology and mating behavior of the Fiery Skipper, *Hylephila
phylaeus* (Hesperiidae), Amer. Midl. Nat. 98 (1):85-94.

*Dubi Benyamini*, *91 Levona Str. Bet Arge, D. N. Moddin, Israel, 71947.*

## Book Reviews

THE BUTTERFLIES OF THE WEST INDIES AND SOUTH FLORIDA. 1994. D. Spencer Smith, L. D. Miller & J. Y. Miller Oxford University Press, 264 pp, 32 plates: publication date 28 April 1994; Cloth ISBN: 0-19-857199-2; Cloth Price: $125.00

To many people the Caribbean islands will always evoke a romantic visage of paradise; where palm trees dripping orchids sway along unspoiled beaches, and elegant birds chatter in the forest dark amidst swirls of brightly colored butterflies. Tough to grasp the fact that most of those tropical islands will soon be devoid of relatively intact habitats and their species associations, but brimming with industrial waste, air conditioned hotel comfort, and only fading memories of what it was like. Thus, at a time when information on the diverse Caribbean islands is needed more than ever, *The Butterflies of the West Indies and South Florida* arrives to help fill a substantial void in our understanding of butterflies and skippers. In many respects this book supersedes three books: Brown & Heinemann (1972), Riley (1975), and Schwartz (1989). But this attractively printed book's long-term contribution is that it represents a modern means of identifying the butterflies and skippers of the Caribbean region, all under one cover.

The five brief introductory chapters cover the West Indies and South Florida and its butterflies (including biogeography and the size of island faunas), conservation, and a very nice review chapter on the history of collecting and collectors of the islands. Even though it may have been a temptation to devise and include them, common names of butterflies were omitted. This was a relief to see. Instead, we are given a complete taxonomic checklist of the butterfly fauna outfitted in crisp nomenclature. Finally, there is an appendix (which could have followed the taxonomic checklist) that allows the reader to assign the plant genera mentioned in the text to their proper families. Although a trifle brief for my tastes, the information will be welcome to the users of this book.

The real heart of this volume, and what will be read by everyone who owns this book, is nested within the treatments of the butterflies themselves. Starting with a brief synopsis of each higher level category (family to subfamily, and genus), the reader arrives at the species account. The species accounts commence from fairly detailed and technical descriptions (with diagnostic characters italicized) followed by range information and natural history observations, followed in turn by short descriptions of subspecies (where applicable), and conclude with informative snippets on taxonomy, distribution, natural history and queries about each species. In short, there is a wealth of information here that is accessible and useful to an audience ranging from the novice to the butterfly cognoscenti.

Faced with the often formidable problem of identifying specimens of varying quality, users of this book will have the distinct pleasure of using color plates derived from the paintings of Richard Lewington. To say that the identification plates are good would be a disservice - they are excellent, and, perhaps, a benchmark for modern field guides. Lewington's artwork does not merely create caricatures aimed at identification, but it manages to capture the subtle essence of the butterflies themselves. An additional bonus is that the medium format of the book sets off the beauty and utility of these plates to advantage.

Although generally well written, the text contains a sprinkling of some unusual sentence structures. For example, in an apparent encapsulation of some quotes found in Brown & Heinemann (1972), something seems to have been lost in the translation: "...They cite Walker's notes (unfortunately too lengthy to reproduce here) on the behavior of H. orion adults, as they approach and feed on 'apple' fruit remaining on the tree, but damaged by bats, that makes museum specimens conspicuously incomplete records of a butterfly species!... (p.74)" Huh? This example (and a few others elsewhere) suggest lines dropped in the proofs, and here one is obligated to finger-wag at editorial oversights. The occasional odd sentence structure aside, there is much to be gleaned from this treatment of the Caribbean butterfly fauna.

There are three areas where, in my opinion, this book fell down: the price of the book, the manner in which higher classification was employed, and the treatment of butterfly biology at all levels. My spasm about price is simple - it greatly restricts the audience that will be able to buy this book in two ways. Let us be honest. Yes, American and European countries are covered (primarily libraries), but the probability is low that the publisher will distribute the book where it should be available: in the West Indies. Even if a distribution miracle should come to pass, how many of the potential students of butterflies living in the West Indies (or elsewhere for that matter) will be able to afford a book that costs $125? Another way of phrasing this would be to ask, How is it possible for an academic press to publish a potentially popular, but relatively slim field guide, and expect it to sell at such a price? To the publisher I would direct the query, Can we anticipate a paperback edition?

Classification, systematics, phylogeny, taxonomy, cladistics. All terms that are common in the biodiversity communication channels, be they academic or not. We are told that the higher classification employed in the book is "traditional". To me the higher classification is not at all traditional, and rather apathetic in the bargain. Some might argue that whether the milkweed butterflies are considered as a family (as in this book) or as a subfamily (my idea of traditional) is trivial fluff. If Danaidae, Ithomiidae, and Satyridae are elevated as families, however, it is inappropriate not to divide the residual Nymphalidae into similar ranks (i.e., Apaturidae, Charaxidae, etc.). Come on, two of the authors are formally trained systematists. Lumping or splitting aside, whatever classification is used, at the very least the users of this book deserve to know about the existence of other systematic arrangements - especially the incipient butterfly biologists and systematists. Thus, it is a mystery to me why the broadly relevant volume edited by Vane-Wright & Ackery (1989), a work that contains wide ranging summaries of butterfly systematics (and biology), was only mentioned in passing in the preface, and not even given an accessible citation. It would have been so easy to include it. This is a glaring oversight.

Given the scope and potential of *The Butterflies of the West Indies and South Florida*, its coverage of general biology and natural history at all taxonomic ranks was disappointing. References to the biological traits at the family level are indolent to non-existent, and give the impression that general butterfly biology is either pedestrian or extraneous. At the species level, the coverage of life histories is uneven, and in some cases may obfuscate the trail to available literature. Despite what a significant number of the species accounts imply, there is considerable published information directly relevant to the natural history of the West Indian butterfly fauna. Two examples. The life history of *Historis odius*

is an excerpt from Brown & Heinemann (1972), but why no mention of Muyshondt & Muyshondt (1979) who provide comparative illustrations of the early stages in some detail? Under *Hypna clytemnestra* we are informed that the life history is unknown. However, the work of Young (1982) on this species, complete with illustrations, is strong evidence to the contrary. Although such life history information may not have been derived from work conducted in the West Indies directly, it is puzzling why the authors chose not to be more thorough or helpful to the novice who may not have access to well stocked libraries. Again, a direct citation to Vane-Wright & Ackery's volume would have gone a long way toward providing the curious reader an entrance to a substantial literature. In future editions the authors might consider adding an addenda bibliography pertinent to systematics, natural history and ecology.

Conservation biologists, taxonomists, biogeographers, and simply the curious naturalist now have a reference work that should stimulate more detailed work on the butterflies of the West Indies. The authors and the artist of this volume are to be congratulated for uniting their different perceptions and approaches to the study of butterflies. So here I am at the bottom line as a book reviewer. My thoughts go as follows. The prospective reader of *The Butterflies of the West Indies and South Florida* should recoil at the price, spend the money if you can, start collecting other literature pertinent to butterfly systematics and biology, and use this book as an identification guide. Me? I hope we all begin learning more about West Indian butterflies.

*P.J. DeVries, Dept. of Biology, University of Oregon, Eugene, Oregon 97403*

## LITERATURE CITED

BROWN, F. M. & B. HEINEMANN 1972. Jamaica and its butterflies. Classey, London.

MUYSHONDT, A. & A. MUYSHONDT JR. 1979. Notes on the life cycle and natural history of the butterflies of El Salvador IIc. *Historis odius* and *Coea acheronta* (Nymphalidae: Coloburinae). J. Lep. Soc. 33: 112-123.

RILEY, N. D. 1975. A field guide to the butterflies of the West Indies. Collins, London.

SCHWARTZ, A. 1989. The butterflies of Hispaniola. Univ. of Florida Press, Gainesville.

YOUNG, A. M. 1982. Natural History of *Hypna clytemnestra* Cr. (Nymphalidae) in Costa Rica. J. Lep. Soc. 36:310-314.

VANE-WRIGHT, R. I. & P. R. ACKERY (eds.) 1989. The biology of butterflies. Symp. Roy. Ent. Soc.11: 1-429. Princeton Univ. Press, Princeton.

SWALLOWTAIL BUTTERFLIES OF THE AMERICAS / A STUDY IN BIO-LOGICAL DYNAMICS, ECOLOGICAL DIVERSITY, BIOSYSTEMATICS AND CONSERVATION. 1994. by Hamilton A. Tyler, Keith S. Brown, Jr. and Kent H. Wilson. Scientific Publishers, Inc., Gainesville, Florida . 376 pp. ISBN 0-945417-90-X (cloth) Price: $49.50

Once in a while something new comes along to jolt us from our sleepy traditions. The recent book *Swallowtail Butterflies of the Americas* by Tyler, Brown and Wilson (hereafter abbreviated as SWABA) is not for everyone - especially not the traditionalist. Overwhelming (and at times exhausting), this book is a force to be

reckoned with. In its challenge to traditionalist approaches, SWABA reminds me of the ferocious jazz piano of Cecil Taylor on his mid 1960's compositions entitled "Unit Structures" - complex cascades of rhythm and sustained flights of innovation. The style that courses from every surface of SWABA is manifestly Brown's, the dynamo behind this tour de force. Indeed, the contributions of Tyler and Wilson, like the sidemen in a Cecil Taylor trio, are all but eclipsed by the Brownian vortex that is everywhere at once. Comparable to a Cecil Taylor performance, the reader of SWABA is at once dominated by an energy that above all demands an open mind. That is to say, one is carried along for the ride wherever it may take you.

The sheer quantity of taxonomic, systematic, morphological, chemical, ecological, evolutionary, genetical, historical, gazetteerical, philosophical and mythical information that is detailed, covered, treated, alluded to, whisked over, and hinted at in SWABA is staggering. As a matter of fact, the ONLY physical surface of this book that does not have information packed onto it faces the dedication. This page is innocently blank. A synthesis of everything that has gone before it, SWABA is now the source for information on the New World Papilionidae. Bristling with tables, appendices, matrices, graphs, figures, photos, and color plates depicting every conceivable aspect of the American Papilionidae, the publication of SWABA heralds a distinctly new type of book on butterflies. By bringing together a massive amount of information the authors have provided a monumental service to insect biology in general, and swallowtail biology in particular that will not soon be repeated.

The energetic style of SWABA can be both stimulating and baffling. I found the sections on early stages and the many "Do it yourself" sections ending each chapter particularly inspiring, but I remain puzzled in trying to make unified sense of Figs. 5.2 - 5.5 on host plant relationships, and the Fastkey to adults proved frustrating - simply too much information crammed in there. With perseverance I suspect that finding one's way around may be easier, and prove more edifying. The truly original chapter on systematics and its schools in SWABA should be read by everyone interested in organisms and systematics. This section does an entertaining, even-handed job of laying it all out for the reader: a paradoxical mix where cladists, pheneticists, evolutionists and creationists all get equal time. However, one might grumble that SWABA does not seem to provide diagnostic characters for the various genera, species or other taxonomic categories. That is to say, if *Pterourus* or *Heraclides* really are appropriate generic names to be used for various familiar *Papilio* species, one wants to see evidence in the form of characters as to why this is so, not just, 'trust me I know'. This brings us to what I feel are problems with SWABA.

As a means of identifying and retrieving information about specific butterflies, this book is diabolically user-hostile. The organization and layout requires wading repeatedly from the index through multiple pages and legends, and back again. Even when familiar with a particular species, I often gave up in frustration rather than continually chase about all the various pages to see what SWABA had to say. Two graduate students (one a novice, and one who knows a little about butterflies) were given the volume and asked to identify some specimens of *Parides erithalion* and *Protesilaus protesilaus*. After an hour or so one stated, "...this is a nightmare. I give up. I can't even find the names for the illustrations". The novice took longer, but eventually returned saying, "Sorry, I'm not sure if these are identified correctly or not (they weren't). Is butterfly taxonomy always

so complicated"? At this point we must ask, why this navigational nightmare in SWABA for something so simple as identifying butterflies from color plates?

The intractable nature of the identification plates stems from the combination of two types of plates, and their legends. One type of plate (which could and should have been omitted) is composed of crudely cut-and-pasted poor quality photos with each specimen designated by a letter. This faces another, good quality plate that is composed of specimens oriented at various odd angles, at times oddly numbered, and that may or may not be relevant to the lettered plates. However, the *coup de grace* is that not only do the plate legends nearly require a microscope to see the abbreviations and codes, but also they are often on completely different pages, lost amidst other captions and legends. Even though these legends bear footnotes that attempt to guide the user, they are often unhelpful in the game of hide and seek one has to play simply to put a name on an illustrated specimen. This just doesn't inspire user confidence in arriving at determinations.

To my mind, the persons at Scientific Publishers, Inc., P. O. Box 15718, Gainesville, Florida 32604 who are responsible for the layout and editing of SWABA should be confined to a room and forced to determine all of the species in the book from specimens! Cruel punishment no doubt, but under the circumstances, fair. Go ahead, try it. Identify a specimen of *P. protesilaus* or some *Parides* with the book. If you find the key, please tell me or my students how to navigate through SWABA and use it as an identification guide.

Anyone interested in swallowtail butterflies and their role in systematics, ecology, evolution, and conservation biology should buy this book. There is a lot of book here for relatively little money. It will help, however, to have plenty of other references on hand before attempting to master the messages of SWABA's unit structures. Lamentably, much of the power in this papilionid manifesto is hampered by the unorthodox organization and layout. Still, SWABA should be useful to papilionid specialists, butterfly ecologists, and conservation biologists. I look forward to as many profitable hours wrestling with it as I have spent listening to the inventions of Cecil Taylor. Acknowledgments: This manuscript benefited from comments provided by J. Coyne, K. Hope, R. Lande, C. Penz, G. Perry, M. Wood and two grad students who wish to remain anonymous.

*P. J. DeVries*, *Dept. of Biology, University of Oregon, Eugene, Oregon 97403*

BUTTERFLIES AND CLIMATE CHANGE. Roger L. H. Dennis. 1993. Manchester University Press, Manchester (GB), 302 pp., ill. (ca 16 x 24 cm). ISBN 0-7190-3505-8 (Hardback L 50.00), ISBN 0-7190-4033-7 (Softback £19.99).

It is an established fact that our climate is changing. From time to time some of our more or less helpless politicians talk about it and various green movements present new horror scenarios. It is also an established fact that the climate of Earth keeps changing more or less continuously; at different times Europe was both much warmer and much colder than now and the present average values have not reached those of the post glacial optimum, a period presumably decisive for the forming of the present European ranges of most butterfly species. It is no secret that without drastic measures to cut the ever accelerating growth of human populations in most third world countries, the warming of Earth's atmosphere can not be slowed down. We (and above all the next generation) will

have to learn to live in new conditions whether we like it or not. It will then be too late to discuss in retrospect who is responsible for what: politics is an art of the possible in one particular moment.

In this context the book under review appears to be even more important and timely, and it is an exceptional book by all standards. Butterflies, surely the best researched invertebrate group, are possibly the most important "bio-indicators" of climatic change. Roger Dennis, an acknowledged British butterfly biogeographer and ecologist, explains the interactions between butterfly individuals and populations on the one hand and on the other, the atmospheric systems in which they live and which impose constraints upon their activities. In one of the most interesting chapters (Morphological adaptations to climatic gradients), the author attempts to explain how gradients in adult butterfly morphology and color pattern relate to climate gradients. Finally, in the chapters entitled "Past climates and evolutionary history" and "Further atmospheric changes and butterfly populations: predictions and consequences" he examines adaptive responses to climatic change using models to explain past events and to predict the impact on butterfly populations during the global warming. It does not matter that some of the author's discussions can be considered controversial; but what I do find lacking is a more complex European approach with extensive references to the species not represented in Great Britain.

This book constitutes a major contribution to butterfly ecology and biogeography as well as to our understanding of how anthropogenically caused climatic changes affect butterfly distribution, and has implications for effective long term butterfly conservation. The book is a must for every butterfly ecologist and biogeographer and interesting to taxonomists and knowledgeable conservationists. It is packed with information from various disciplines and therefore not easy to read; summaries of the contents of all chapters would have helped the reader to follow and better understand the author's complex conclusions. This is a small criticism in view of the overall result. Roger Dennis deserves our congratulations on his accomplishment and the publishers our thanks for taking the risk of publishing such an unusual book.

*Otakar Kudrna, Karl Straub Strasse 21, D-8740 Salz (Bad Neustadt), Germany.*

OECOPHORINE GENERA OF AUSTRALIA. I. The *Wingia* Group. 1994. I. F. B. Common. Monographs on Australian Lepidoptera: Volume 3, 390 pp +xvi. CSIRO Publications, East Melbourne. ISBN 0-643-05524-X. $US100. Hardbound.

This third volume of the Monographs on Australian Lepidoptera series is the first of a three volume monograph of the Oecophorine moths. Common estimates that there are presently about 1850 valid species names distributed among over 250 genera in the subfamily. He estimates the total fauna will embrace 5000 species! The *Wingia* group of 91 genera are revised in this volume. The group is almost entirely endemic to Australia. Altogether the Oecophorinae represent about 20% of the Australian Lepidoptera. Most species are believed to have evolved within Australia from Gondwanan ancestors and most use the "dry fruit" members of the Myrtaceae as foodplant. Many species feed on dead *Eucalyptus*

leaves. The high diversity of the group and often dense populations imply they are important to recycling leaf litter of these refractory plants into humus.

The revision includes detailed information on genitalia of both sexes, distribution and biology. A total of 500 valid species names are referred to, with an additional 268 undescribed species identified in collections. Thirty-five of the 91 genera are new.

A preliminary phylogenetic analysis was attempted using Hennig86, but several subgroups remain unresolved with some anomalous genera. There are 712 high quality figures, mostly photographs of adults and their genitalia.

The work greatly advances our knowledge of this speciose subfamily while emphasizing the enormous task yet remaining before we have a comprehensive understanding of biodiversity on our planet.

*Rudolf H. T. Mattoni*, *Department of Geography, UCLA, Los Angeles, CA 90095-1524.*

THE EMPEROR MOTHS OF NAMIBIA, by Rolf Oberprieler, 1995. Ecogilde cc, P. O. Box 178, Hartbeespoort 0216, South Africa, ix + 91 pages, including 30 color plates. Hardcover, 18 X 24.5 cm. ISBN 0-9583889-2-X. Price: about $45 US.

Namibia (formerly Southwest Africa) is a large country in southern Africa with a coastline along the Atlantic Ocean. Despite its large size, the saturniid fauna is somewhat depauperate due to the arid climate. The author Rolf Oberprieler, an entomologist in Pretoria, was a long-term resident of Namibia and has done an outstanding job of documenting the Saturniidae of this region. There are 25 species known from that country, plus three that are likely to occur there. The text for each species covers the basics, and on the facing page are color photographs of pinned adults and, in many cases, mature caterpillars. Photographs in introductory chapters show eggs, cocoons, young larvae, and live adults. The author is an accomplished photographer and the color reproduction of his photographs is good but not excellent. I did not find misspellings or typographical errors. The book is well-organized.

Oberprieler discusses the collecting history of the region, a discussion which is entirely eurocentric by necessity. He also gives brief discussions on the ecology, biology, and conservation of these moths. He then describes the ecosystems of Namibia as they relate to the distributions of the saturniids. Another introductory chapter deals with collecting, preservation, and rearing of specimens. The ideal reader of the book would be an amateur entomologist who is a resident of southern Africa. However, considering the worldwide popularity of these big moths and the literature about them, I am sure many copies will be sold outside of Africa. There is almost nothing available that is not out-of-print on the saturniids of Africa. Use these reasons plus the abundant color photographs to justify paying the price.

*Richard S. Peigler*, *Denver Museum of Natural History, 2001 Colorado Blvd., Denver, CO 80205-5798*

HOW TO PHOTOGRAPH INSECTS & SPIDERS / BUTTERFLIES • DRAGON-
FLIES • GRASSHOPPERS • MILLIPEDES • SCORPIONS..., 1994. Larry West
and Julie Ridl. Stackpole Books, Mechanicsburg, PA, 128 pp, 92 color plates;
ISBN 0-8117-2453-0 (softcover). Price: $16.95

As a wildlife photographer of many years, nothing strikes more fear in my heart
than having to photograph insects. Not that I'm afraid of getting stung or
anything like that. But it's the work and challenge of getting down and close to
a prey more ellusive than the swiftest bird or predatory mammal. The years of
experimentation just to get the techniques down have stopped me from ever
venturing into this fascinating and intriguing world.

Much to my relief, Larry West and Julie Ridl have opened doors to insect
photography with this book. They have done an excellent job of taking years of
experimentation out of the insect photography equation. Any question on
techniques for photographing the smallest of our many-legged friends is an-
swered in these pages.

The book starts with an inspiring section on the challenges and rewards of
insect photography. It opens the doors of the creative mind to the possibility of
finding more in the Florida Everglades than herons and alligators. It offers up the
possibilitiy of finding a mosquito that holds its legs in a unique fashion or of
offering your hand as a bait in hopes of photographing ellusive quarry.

After inspiring us to stop and look in the first chapter, West and Ridl take us
in the next into the equipment needed to quench our new thirst. The text does an
excellent job of defining the equipment needed to be successful at bug photogra-
phy. It goes further in additional chapters in applying that equipment to specific
problems and their solutions. From my point of view, insect photograpyhy is one
big problem made up of thousands of little ones. West and Ridl are to be
commended for making mincemeat of these little problems, making it possible to
literally go right into the field and successfully photograph whatever creatures
we might come across.

Probably the most rewarding and educational aspects of the book are the rich
illustrations and their captions. Great effort is made to accurately depict what
went into the making of the photographs. You could just look at the photographs
and read their captions and learn more on insect photography than previously
written in other books.

The topic is summarized beautifully in the last chapter by helping us better
understand the insect world in which *we* live. It not only helps us get a foot up on
understanding them and where they live, but our responsibility towards them.
The ethics discussed behind creating the images is timely as well as insightful.

Larry West and Julie Ridl did us all a big favor. They did more with their book
than explain the many mysteries intrinsic to insect photography. They opened
the doors for all of us with cameras to explore the minute world that surrounds
us. They make it possible to find subjects no matter where we are, city or
wilderness, and turn them into giants that can shake the world. I'll be darned if
I'm going to give up my copy of the book. I suggest you go out and get your own!

*B. "Moose" Peterson*, *Wildlife Research Photography, P.O. Box 30694, Santa
Barbara, CA 93130*

# INSTRUCTIONS TO AUTHORS

**Manuscript format:** At the time of initial submission, Two copies *must* be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. If possible italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All **measurements** must be metric. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (e.g. 6.IV.1995). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

**Electronic submission:** The Journal is now being produced via desktop publishing, allowing much shorter publication times. Although typewritten manuscripts are acceptable, those submitted on computer disk are *highly* preferred. After being notified of your paper's acceptance, submit either a Macintosh or IBM disk (3.5 inch) version. Include on your disk both the fully formatted copy from your word processing program and a text-only (ASCII) copy. The preferred format for text is Microsoft Word, although translation utilities will allow conversion from most formats. Put returns only at the ends of paragraphs, not at the end of each line. Use one tab to indent each paragraph. Even if your printer is incapable of outputting italics, please specify italics rather than underline in your disk copy. Please note in your cover letter any special characters that are used in either the body of the text or the tables (e.g. é, ü, °, §, µ, ♂, ♀). All figures which are prepared on the computer should also be submitted electronically. Please include these figures in a standard interchange format such as EPS or TIFF.

**Title material:** All papers must include the title, author's name, author's address, and any titular reference and institutional approval reference. A **family citation** *must* be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

**Abstracts and Short Papers:** All papers exceeding three typed pages must be accompanied by an abstract of no more than 300 words. Neither an additional summary nor key words are required, although key words are recommended.

**Name citations and Systematic Works:** The first mention of any organism should include the full scientific name with unabbreviated author and year of description. There *must* be conformity to the current International Code of Zoological Nomenclature. We strongly urge depositing of types in major museums, all type depositories must be cited.

**References:** All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations should not be used; write out the entire journal name. Do not underline or italicize periodicals. If four or less references are cited, please cite in body of text not in Literature Cited. For multiple citations by the same author(s), use six hyphens rather than repeating the author's name.

**Tables:** When formulating tables, keep in mind that the final table will fill a maximum space of 11.5 by 19 cm either horizontally or vertically oriented. Number tables with Arabic numerals. When submitting tables on disk, use tabs between columns rather than multiple spaces.

**Illustrations:** Color can be submitted as either a transparency or print, the quality of which is critical. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors *must* plan on illustrations for reduction to page size. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink. Include a metric scale. Each figure should be cited and explained as such. Each illustration must be identified by author and title on the back. Indicate whether you want the illustration returned at your expense. Retain original illustrations until paper is accepted. **Legends** should be separately typed on pages entitled "Explanation of Figures." Number legends consecutively with separate paragraph for each page of illustration.

**Review:** All papers will be read by the editor(s) & submitted for formal review to two referees.

**IN THIS ISSUE**

Date of Publication:    November 1, 1995

COVER ILLUSTRATION: Mating pair of *Hylephila signata*, Santiago Chile, 10
December 1993. Photograph by Dubi Benyamini. See "New courtship posture in
females of two Chilean butterflies: Rejective or receptive?", p. 291.